BIODIVERSITY AND ECOSYSTEM FUNCTIONING: THE EFFECTS OF TREE AND LITTER DIVERSITY

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I dedicate this work to my great grandfather, who always saw nature with the fascination of a child.

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General Introduction

The functional importance of biodiversity for ecosystem processes

Over the last decades, communities and ecosystems globally have undergone dramatic changes due to anthropogenic activities, accompanied by rapid declines and changes in biodiversity at all levels, from biotopes to species and genetic variation contained within species. This has boosted ecological research to understand the functional importance of biodiversity as a regulator of ecosystem processes, dynamics and functioning as well as the consequences of its loss (reviewed by Kinzig et al. 2002, Loreau et al. 2002b, Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006, Cardinale et al. 2007). Driven by the question: "Does biodiversity matter for ecosystem integrity, functioning, and the ecosystem's provision of goods and services to humanity?" (Schulze and Mooney 1993), researchers have accumulated evidence for a positive relationship between biodiversity and ecosystem functioning in the past decade (e.g. Hooper et al. 2005, Srivastava and Vellend 2005, Balvanera et al. 2006, Cardinale et al. 2006, 2007).

Ecosystem processes such as primary productivity (e.g. Hector et al. 1999, Tilman et al. 2001, Roscher et al. 2005) and invasion resistance (e.g. Tilman 1997, Knops et al. 1999, Naeem et al. 2000), defining ecosystem stability and resilience (e.g. McCann 2000, Loreau et al. 2002a), have been reported to be positively affected by biodiversity. Furthermore, it is increasingly recognised that biodiversity can simultaneously enhance multiple ecosystem processes and thus is required to maintain multifunctional ecosystems (Hector and Bagchi 2007). A preponderance of studies has however focused on biodiversity at the species or the functional group level, thus neglecting intraspecific genetic variation, the variation that matters not only to evolution but also to ecology (Dawkins 1979, 1982). Intraspecific genetic variation as well genetic diversity (i.e. the amount of genetic variation present) can have wide-ranging ecological consequences for ecosystem processes and functions (Whitham et al. 2003, 2006, Madritch et al. 2009). It has

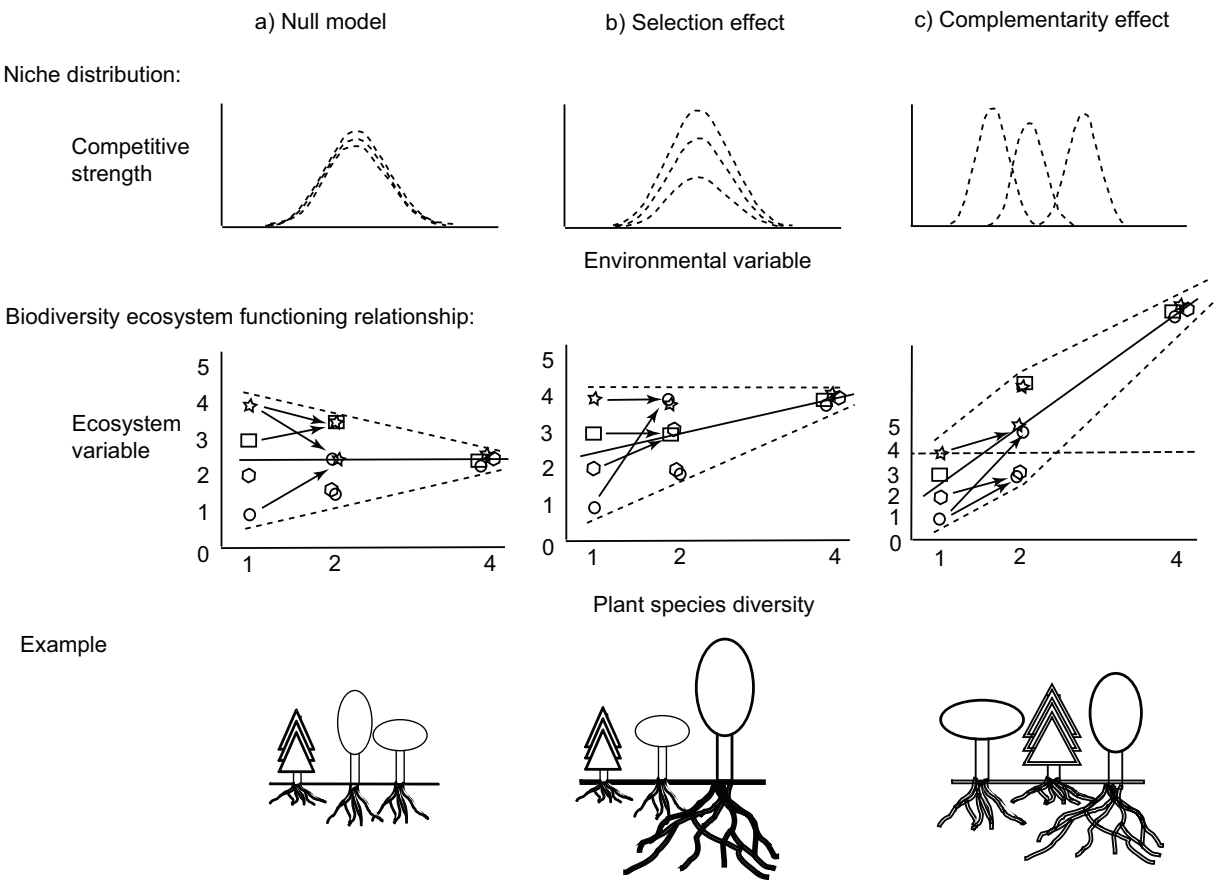

Fig. 1. The figure (adapted from Schmid 2003) presents three different scenarios for the relationship between biodiversity and ecosystem functioning. The first row shows the relative positions of the niches of different species along an environmental gradient, and their relative competitive strength. The second row shows the expected relationship between biodiversity and ecosystem functioning for each scenario. The four symbols represent different species, which in species mixtures are overlaid. Arrows indicate which species are combined in a given mixture. The null model includes only additive effects of mixing species, i.e. mixture performance is the mean of the component species. Given the selection effect, the mixture performance is largely determined by species with particular traits that come to dominate the community. A positive selection effect, i.e. higher-than-average monoculture performance, is presented here. Complementarity arises when the community performance is enhanced through niche partitioning or direct positive interactions (facilitation).

been shown for example that intraspecific genetic diversity in plants determines the diversity of associated invertebrate communities above and below ground as well as community structure, and increases aboveground productivity (e.g. Crutsinger et al. 2006, 2008). Others have demonstrated the importance of intraspecific genetic variation and diversity for ecosystem

processes such as decomposition and nutrient cycling (e.g. Madritch and Hunter 2002, Schweitzer et al. 2005). These effects were comparable to the effects of plant species diversity observed in other studies and may therefore have important, though under-appreciated, importance in ecosystem functioning (e.g. Schweitzer et al. 2005, Crutsinger et al. 2006).

Although the mechanisms underlying the positive biodiversity ecosystem functioning relationship are still discussed controversially, two mechanisms are widely accepted (Fig. 1). Firstly, as diversity levels increase there is a higher probability of including species with favourable characteristics for the ecosystem function in question (known as the "sampling effect", Aarssen 1997, Huston 1997, Tilman et al. 1997). The sampling effect is a special case of the "selection effect" (sensu Loreau and Hector 2001, and the "dominance effect" of Fox 2005), which can be generalised to include other situations in which particular species (including species with a lower-than-average performance) come to dominate the community. The "selection effect" according to Loreau and Hector (2001) measures the covariance between changes in species relative abundances in mixtures and their performance in monoculture. Nevertheless, the terms "sampling" and "selection" are often used synonymously (Huston 1997, Cardinale et al. 2006). However, in both cases the biodiversity ecosystem functioning relationship is driven by the traits of particular species. Secondly, positive diversity effects might result from niche partitioning or direct positive interactions (i.e. facilitation) among species with different traits, decreasing interspecific competition in more diverse communities (Naeem et al. 1994, Tilman et al. 1996, Loreau 1998). This for example enables resources to be used more efficiently than if one or few species with similar traits compete for the same resources. Both mechanisms are, however, not mutually exclusive and transitions between them may occur over longer time spans (Pacala and Tilman 2002), particularly given the potential for competitive interactions among species to change over time.

Plant competition

Since the earliest days of ecological thinking, competitive interactions both within and among species have been recognized to be among the major forces shaping populations and structuring plant communities (e.g. Clements 1929, Gause 1934). It is commonly assumed that competitive interactions within species are more intense compared with competition among different species, because individuals of one species are generally more similar in their niche requirements (e.g. Goldberg and Barton 1992). This should lead to a stronger response to intra- compared with interspecific competition.

Scientists have studied the evolution of competitive traits and strategies, and it was Darwin himself who studied what we now call behavioural traits in plants (Darwin 1880 in Novoplansky 2009). Besides their limited mobility, plants have the ability to make adaptive decisions and to show considerable plasticity in their physiology and morphology in response to cues and signals they perceive from their environment (Hodge 2009, Novoplansky 2009). This perhaps prompted researchers to draw parallels between animal and plant behavioural mechanisms, since plastic responses related e.g. to resource allocation of each individual in a competitive setting may be dependent on the responses of its neighbours (e.g. Gersani et al. 2001). Those plastic responses regarding foraging for resources are of particular interest, since plant roots contribute to net primary productivity and are important for the regulation of heterotrophic soil organisms and soil carbon sequestration (e.g. Bessler et al. 2009). Therefore, plant competitive behaviour may have implications for processes operating at larger ecological scales (Novoplansky 2009), and for the role of plant competition in determining the diversity and functioning of communities and ecosystems (e.g. Grime 1979, Tilman 1982).

TREE DIVERSITY AND ECOSYSTEM FUNCTIONING

Until now investigations of the biodiversity ecosystem functioning relationship have been mainly limited to grasslands, old-field communities and aquatic or terrestrial microcosm systems (Schmid et al. 2001, Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006, 2007). Consequently, the importance of biodiversity for ecosystem processes and functioning in forest ecosystems still remains poorly understood, despite their overwhelming ecological and socioeconomic importance (e.g. Scherer-Lorenzen et al. 2005, 2007b, Leuschner et al. 2009). Forests (including plantations) cover over 30% of the Earth's surface, store more than 80% of the biomass carbon of the planet and account for 65% of the annual carbon fixation (net primary productivity) (Scherer-Lorenzen et al. 2007b and references therein). However, compared to herbaceous vegetation, forest ecosystems face even more dramatic changes in their biological diversity (WRI 2000).

In European forests, tree species composition and diversity has shifted massively towards mostly monospecific managed stands due to the increasing demand for timber production. Today, conifer species comprise 70 % and broadleaved deciduous species 30 % of the European forests, the reverse of the potential natural vegetation (Körner 2005). Therefore, there is a great need for studying the functional consequences of tree diversity for ecosystem processes and functioning, particularly now as Central European Forestry is conducting a broad-scale conversion of monocultures into mixed forest stands and attempting to re-establish more natural forest communities with less common species (e.g. Gardiner 1999, MCPFE 2003, Scherer-Lorenzen et al. 2005).

Observational and comparative studies have been a vital tool in describing correlations between tree diversity and ecosystem processes across existing forest stands (e.g. Caspersen and Pacala 2001, Szwagrzyk and Gazda 2007, Vila et al. 2007). However, they have often been criticised due to the potential for co-varying factors to confound interpretations and for their inability

to isolate cause and effect in the biodiversity ecosystem functioning relationship (Lawton et al. 1998, Wardle 2001). In contrast, experimental approachs allow the manipulation of tree diversity levels as a response variable, thus investigating consequences of species loss or species addition on ecosystem processes while keeping confounding factors, such as environmental conditions, constant (see Schmid 2002 for a distinction of both approaches). Since silvicultural research focused mainly on monocultures and two-species mixtures (e.g. Kelty et al. 1992, Pretzsch 2005) with highly productive varieties of economically important timber species (Vila et al. 2005), experimental forest plantations manipulating tree diversity over a wider gradient and with less common species are needed to assess the functional importance of tree diversity (Scherer-Lorenzen et al. 2007b).

Today, there are nine large-scale tree diversity experiments encompassing the boreal (Satakunta Tree Species Diversity Experiment, Finland: e.g. Vehvilainen and Koricheva 2006), the temperate (ORPHEE, France, BIOTREE, Germany: e.g. Scherer-Lorenzen et al. 2007b), the sub-tropical (BEF-China: <http://www.bef-china.de/>) and the tropical (Sardinilla Project, Panama: e.g. Scherer-Lorenzen et al. 2007a, Potvin and Gotelli 2008, Sabah Biodiversity Project, Borneo: <http://www.searrp.org/research_sabah_biodiversity.cfm>) zones and another one soon to be established in Belgium (FORBIO, Scherer-Lorenzen personal communication). These plantations are designed to investigate the biodiversity ecosystem functioning relationship at a scale relevant to forest management, but also the mechanisms underlying this relationship (Scherer-Lorenzen et al. 2007b, Healy et al. 2008). However, their focus is mainly aboveground and as far as they do consider soil processes, they marginalise the importance of resource-input to the soil subsystem via dead organic material.

After life effects of tree diversity: Leaf litter

Whereas past research has typically focused on aboveground processes, the “after life effects” (Findlay et al. 1996) of plant diversity on key ecosystem processes belowground, such as

decomposition and nutrient mineralization, only recently became recognized and are still poorly understood (Wardle 2002, Gartner and Cardon 2004, Hättenschwiler et al. 2005). However, most aboveground net primary productivity enters the detrital pathway as plant litter, thereby mediating biodiversity effects aboveground (Coleman and Crossley 1996). Together with belowground plant litter (e.g. dead roots and mycorrhiza, root exudates), these inputs to the soil subsystem constitute the main resource of energy and matter for a highly diverse soil community connected by complex interactions involved in decomposition processes (e.g. Hättenschwiler et al. 2005). The recycling of nutrients and carbon from litter during decomposition is a fundamental ecosystem process that has a major control over nutrient mineralization and availability (Swift et al. 1979, Cadish and Giller 1997). Recycled nutrients available for plant uptake in turn affect plant growth, thereby feeding back on community dynamics and structure as well as ecosystem productivity (Wardle 2002, Bardgett 2005). In managed forests aboveground litter is composed primarily of leaf litter and fine woody debris, whereas tree stems are removed. Thus, nutrient recycling in these systems depend entirely on the input of rapidly decomposed litter components as opposed to the long-lasting effects of wood decomposition in unmanaged forests.

In natural ecosystems, the leaf litter of individual species and individuals within species seldom decomposes in isolation, but rather in mixtures of litter from several species and individuals. However, potential interactions among litters during decomposition have only recently been considered in decomposition studies and a general pattern in mechanisms underlying decomposition in litter mixtures has not yet emerged (Gartner and Cardon 2004, Hättenschwiler et al. 2005). Some studies report decomposition to be increased with increasing litter diversity (e.g. Bardgett and Shine 1999, Hector et al. 2000, Spehn et al. 2005), while others show no or idiosyncratic effects (e.g. Blair et al. 1990, Wardle et al. 1997). These observed diversity effects have been proposed to be caused by nutrient transfer among litter types, stimulation or inhibition of microorganisms by specific litter compounds, and positive feed backs of soil fauna due to greater habitat and food diversity in structurally more diverse litter layers, although experimental evidence is scarce (reviewed by Hättenschwiler et al. 2005). Furthermore, the

Table 1. Characteristics of the tree species planted in the Kreintz Experiment and studied in this thesis.

Tree species	C/N	Litter[1]	pH	Mycorrhiza[2]	Insects[3]	Specialists[4]
Fraxinus excelsior	21	1	6.4	VA	145	44
Tilia cordata	37	2	5.4	VA, Ecto	207	28
Fagus sylvatica	51	3	4.3	Ecto	275	44
Quercus petraea	53	3	4.8	Ecto	699	252
Picea abies	48	3	4.1	Ecto	279	75
Pinus sylvestris	66	4.5	4.2	VA, Ecto	335	157

[1]Half-time for litter decomposition [years], [2]VA: vesicular-arbuscular mycorrhiza, Ecto: ectomycorrhiza, [3]Number of associated phytophagous insects, [4]Number of phytophagous insects specific to the tree genus

Data from: Schulze et al. (1996), Harley & Harley (1987), Brändle & Brandl (2001).

role of litter diversity for the composition, diversity and activity of soil organisms is still poorly understood, as well as the subsequent consequences of the soil food-web structure on ecosystem processes (Wardle 2002, Hättenschwiler et al. 2005).

Linking aboveground biodiversity with belowground processes: The Kreinitz experiment

The Kreinitz experiment in Germany (near Kreinitz, Saxony, 51°23´N, 13°15´E, 95 m a.s.l.), established in November 2005, was specifically designed to link aboveground biodiversity with belowground processes. In this experiment, tree species and aboveground litter diversity and composition are manipulated (1) to study the effects of tree and litter diversity on ecosystem processes and functioning, such as plant productivity, decomposition and nutrient cycling, (2) to quantify the effects of tree and litter diversity on the structure and stability of soil food webs but also (3) on aboveground tree parasites and pathogens.

The experimental plots vary in tree and corresponding litter diversity (one, two, three, five or

six species) and composition (all possible species combinations). Two control plots (no trees or litter) were additionally established, and leaf litter is applied annually at a rate of 600 g m^{-2}. The species pool contains six temperate tree species: *Fagus sylvatica* L., *Fraxinus excelsior* L., *Tilia cordata* Mill., *Quercus petraea* (Matt.) Liebl., *Pinus sylvestris* L. and *Picea abies* (L.) Karst., all native and common in Central European forests, representing economically important timber species. Most of them naturally co-occur in mixtures although not all combinations are equally common. *F. sylvatica* is the dominant deciduous tree in unmanaged forests often growing in almost monospecific stands. In Central European forest plantations, monocultures of *P. sylvestris* and *P. abies* dominate, and *P. abies* has been planted even outside its natural distribution. It is, however, a recognized goal of Central European forestry to increase diversity of managed forests by gradually replacing monocultures of *P. sylvestris* and *P. abies* with more species rich communities of deciduous trees. The litter of the tree species cover a range of decomposition rates, with *F. excelsior* and *T. cordata* having rather fast-decomposing leaf litter, *F. sylvatica* and *Q. petraea* slow-decomposing leaf litter, and *P. sylvestris* and *P. abies* slow-decomposing needles (Table 1). Furthermore, these tree species vary in their type of mycorrhiza and the number of associated aboveground insect species (Table 1).

This thesis was conducted within the framework of the Kreinitz experiment, which was used for some of the studies presented here. In addition to the studies covered by this thesis, I measured tree growth and mortality in the Kreinitz experiment over a period of three years and have been involved with the management of this large-scale field study, in particular helping to coordinate the replanting of trees, and litter collection and application. This work contributes to the long-term monitoring and investigation of the effects of tree and litter diversity on ecosystem processes in this experimental set up.

Thesis outline

The goal of this thesis was to explore whether the positive relationship between biodiversity and ecosystem functioning found in grasslands also applies to temperate tree communities, and whether it can be found for processes occurring both above and below ground. The work was motivated by three fundamental questions:

(1) Does tree diversity positively affect ecosystem processes?

(2) Are diversity effects consistent across different ecosystem processes?

(3) Are tree diversity effects also important at the intraspecific level?

Due to high initial mortality of tree saplings and repeated replacement of dead individuals, the Kreinitz experiment was limited in the extent to which it could be used to address these questions within the time frame of this thesis. Furthermore, the field experiment is only partially suitable to directly measure and quantify effects of tree diversity below ground and therefore I established further pot experiments to complement the field approach. Moreover, additional experiments aimed at understanding specific processes were performed, one of which (chapter 3) was conducted within the Kreinitz experiment. For the pot experiments I used substrate from the field site and the same set of species as used in the Kreinitz experiment so that the findings can be directly linked to the results emerging from the long-term field experiment.

Chapter 1 reports the results of a pot experiment in which I manipulated the number of tree species and their composition to study their effects on productivity. Specifically the aim was to quantify the relative contributions of complementarity and selection to net effects of tree diversity on productivity. Furthermore, I varied community planting density to test its influence on the relationship between tree diversity and productivity, a confounding factor often overlooked in biodiversity research. Allowing destructive harvests, this approach has the particular strength of allowing the quantification of diversity effects and underlying mechanisms below ground.

Chapter 2 focuses specifically on species interactions occurring below ground, namely root competition. Herbaceous plants can sometimes overproduce roots and intensify root allocation in response to neighbouring roots beyond a level that would be optimal for the individual growing along. I investigated whether this competitive strategy also applies to trees. Moreover, I test whether trees react specifically to different neighbouring species, hypothesising that the effect of root overproduction in response to belowground competition is more intense for intra- compared to interspecific competition.

Chapter 3 explores the "after life effects" of tree diversity: the significance of leaf litter species diversity for a key ecosystem process, decomposition. I performed three complementary decomposition trials within the Kreinitz experiment to disentangle the different direct and indirect pathways through which litter diversity acts on decomposition processes, an attempt seldomly made in litter diversity experiments. Furthermore, I studied the functional importance of soil fauna for litter decomposition along this diversity gradient.

Chapter 4 assesses effects of intraspecific variation and diversity on decomposition processes, an important aspect rarely considered in biodiversity research. I choose European beech (*Fagus sylvatica* L.) as a model system to investigate variation in litter quality and decomposition among and within populations and whether litter quality affects decomposition. Furthermore, I test the effects of intraspecific diversity (i.e. mixing of litter individuals) on decomposition, hypothesising that decomposition rates would be faster in mixtures with a higher intraspecific diversity.

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Chapter 1

Positive effects of tree diversity on productivity are density-dependent

Josephine Haase, Harald Auge, Andy Hector, Daniel Prati

Abstract

Evidence is accumulating that plant diversity positively affects productivity in grasslands. Whether diversity also increases forest productivity has hardly been studied, despite the huge ecological and economic importance of forest ecosystems. Furthermore, although it is well known that density influences intra- and interspecific interactions, its impact on the relationship between diversity and ecosystem functioning has largely been neglected. This is especially true for ecological interactions occurring below ground.

We planted six temperate tree species in monoculture and mixtures (two, three and six species) at two densities (six or twelve individuals per pot) to investigate the effects of diversity, species composition and density on tree growth, productivity and the underlying mechanisms. After two years of growth, total productivity was increased in mixed compared to monospecific stands. Diversity effects occurred below rather than above ground and were density-dependent. These positive diversity effects were more pronounced at low density and were related to complementarity rather than to the selection effect.

Increased productivity at higher tree diversity has important implications for the management of forests for timber production and as carbon sinks. We emphasise, however, that tree spacing and species composition are crucial considerations when implementing the concept of mixed stands in silviculture.

Key words: belowground interactions, biodiversity and ecosystem functioning, density, productivity, temperate trees, trees, tree growth

Introduction

Evidence for a positive relationship between biodiversity and ecosystem functioning, particularly regarding productivity and nutrient retention, has been accumulating in recent years (see recent reviews by Hooper et al. 2005, Srivastava and Vellend 2005, Balvanera et al. 2006, Cardinale et al. 2006, 2007). Positive effects of biodiversity on productivity have been related to (1) "complementarity" (Naeem et al. 1994, Tilman et al. 1996, Loreau 1998) and (2) "sampling" (Aarssen 1997, Huston 1997, Tilman et al. 1997; similar to the selection/dominance effect in Loreau and Hector 2001 and Fox 2005, see below). Complementarity can arise when individual species differ in their resource use (or another niche axis) or when they interact positively with each other (facilitation), leading to a higher community-performance than expected from performance in monoculture. The sampling effect describes the increased probability of including a particularly high performing species which comes to dominate a community when the number of species rises. In this case the community-performance should not exceed that of the best performing species in monoculture. The selection effect (Loreau and Hector 2001; or dominance effect, Fox 2005) is similar to the sampling effect but relates the relative abundance of species in mixtures to their performance in monoculture (Hector et al. 2009). Positive selection effects occur when species with higher-than-average monoculture biomass come to dominate in mixtures and negative selection effects with the opposite relationship (Hector et al. 2009).

So far investigations in terrestrial systems have been mainly limited to grasslands and old-field communities, where complementarity seems to be the dominant force driving the positive biodiversity ecosystem functioning relationship (e.g. Spehn et al. 2005, Cardinale et al. 2007). Currently there is growing interest in studying this relationship and assessing whether the same holds true for forest communities (e.g. Orians et al. 1996, Scherer-Lorenzen et al. 2005a, 2007, Ewel and Mazzarino 2008, Potvin and Gotelli 2008, Leuschner et al. 2009). However, some methods (e.g. additive partitioning, Loreau and Hector 2001, tripartite partitioning, Fox

2005) developed to quantify the relative contributions of complementarity and selection to net biodiversity effects on ecosystem functioning require that all species grown in mixtures are also grown in monoculture (but see Hector et al. 2009), which is logistically challenging in long-lived forest communities. Furthermore, the potential influence of confounding effects of community density on the biodiversity ecosystem functioning relationship and expression of complementarity and selection has largely been neglected in biodiversity studies so far (but see Polley et al. 2003, He et al. 2005 for grassland studies). This, to our knowledge, is particularly true for forest communities. However, increasing density may in part compensate for low diversity (He et al. 2005) and may amplify selection effects by intensifying species interactions (Polley et al. 2003).

Recently established experimental forest plantations manipulating tree diversity are a useful tool to investigate underlying mechanisms of the relationship between biodiversity and ecosystem functioning (e.g. Scherer-Lorenzen et al. 2005b, 2007, Potvin and Gotelli 2008), but they are often limited in their ability to do so below ground. However, belowground species interactions define resource exploitation and thereby to a large extent also ecosystem productivity and sustainability (e.g. Cannell et al. 1992, Kelty et al. 1992, Jose et al. 2006). Furthermore, interactions below ground may have implications for forest management as well as forest dynamics and carbon sequestration in the face of climate change (e.g. Dhôte 2005, Gleixner et al. 2005, Mund and Schulze 2005). Nevertheless, these interactions have received very little attention. The approach of establishing pot experiments, as a complement to long-term field experiments, has the strength of allowing direct measurements of productivity through destructive harvests, of assessing the potential influence of confounding effects of planting density on the relationship between biodiversity and ecosystem functioning, and particularly of allowing the investigation of underlying mechanisms below ground. Necessarily, investigations are restricted to early stages of tree growth. However, the establishment period may be crucial for the development of biodiversity ecosystem functioning relationships, as has been shown for herbivore pressure, which is lower in young mixed compared to young monospecific stands

(Vehvilainen and Koricheva 2006, Scherer-Lorenzen et al. 2007).

This study was stimulated by recent changes in Central European forest policy, which increasingly favours the planting of mixed forests over pure monocultures and the establishment of less common species (Gardiner 1999, MCPFE 2003, Scherer-Lorenzen et al. 2005a). By establishing tree communities differing in diversity, composition and density in pots, we addressed the following questions:

(1) Does stand productivity increase with increasing levels of tree diversity?

(2) What are the relative contributions of complementarity vs. selection to net biodiversity effects?

(3) How does tree density affect the relationship between biodiversity and ecosystem functioning and its underlying mechanisms?

(4) To what extent are tree diversity effects on productivity determined by mechanisms occurring below ground relative to above ground?

METHODS

Study System

To study the effects of species diversity and density, we selected six temperate tree species: *Fagus sylvatica* L., *Fraxinus excelsior* L., *Tilia cordata* Mill., *Quercus petraea* (Matt.) Liebl., *Pinus sylvestris* L. and *Picea abies* (L.) Karst.. These species are native, common trees in Central European forests and represent economically important timber species. Most of them naturally co-occur in mixtures although not all combinations are equally common. *F. sylvatica* is the dominant deciduous tree in unmanaged forests often growing in almost monospecific stands. In Central European forest plantations, monocultures of *P. sylvestris* and *P. abies* dominate, and *P. abies* has been planted even outside its natural distribution. It is, however, a recognized goal of Central European forestry to increase diversity of managed forests by gradually replacing

monocultures of *P. sylvestris* and *P. abies* with more species rich communities of deciduous trees.

Saplings of each tree species were obtained from a nursery (Fürst Pückler, Zeischa, Germany) and were from the same region as the substrate used for our experiment. The substrate was taken from the upper 10 cm soil horizon of an old fallow site (Kreinitz, Saxony, Germany, 51°23´N, 13°15´E, 95 m a.s.l.) which is currently afforested with the same set of tree species. The soil at that site is characterized as a nutrient poor sandy Cambisol, with a pH of 7.47 and initial nutrient contents of 0.869 % organic carbon, 0.078 % nitrogen and 89.7 mg kg^{-1} plant available P. At planting, species varied in age (one to three years old) and height (15-40 cm), although all individuals of one species were of the same age and approximate height. The initial age and size of trees was similar to that of saplings commonly used for reforestation.

Experimental Design

In April 2006, the saplings were planted into 130 L pots (60 cm diameter, 47 cm height) at two densities (six and twelve individuals per pot at low and high density, respectively). Trees at each density level were equally spaced and planted in a regular pattern (Scherer-Lorenzen et al. 2005b). The assignment of individual species to planting positions within a pot varied among blocks in order to randomize potential neighbourhood effects on ecosystem variables (Pacala and Deutschman 1995, Stoll and Prati 2001). A diversity gradient was established by planting individuals from all six tree species in monocultures, two-, three- and six-species mixtures, including the 15 possible two-species and the 20 possible three-species mixtures. Each combination of density and the 42 different species compositions (6 monocultures, 15 two-species and 20 three-species mixtures, and one six-species mixture) was replicated four times in a randomised block design, resulting in a total of 336 pots with 3024 trees.

Prior to planting, each pot was filled with 3 cm gravel (8-16 mm) and 3 cm sand (0-2 mm) to ensure drainage, and ca. 100 L of sieved substrate. The pots were then placed outdoors in an

experimental garden in Bad Lauchstädt, Germany (51°24´N, 11°53´E, 118 m a.s.l.). During the first growing season, the experimental garden was covered with shade cloth (reduction of light by approximately 45 %) and during winter the pots were embedded in straw to prevent frost damage to the roots. Infestation of trees by fungal pathogens and herbivores was treated using Ortiva (Syngenta, Germany) and Neudosan (Neudorff, Germany) as necessary (i.e. potential diversity effects via natural enemies (Petermann et al. 2008) were not examined), and trees were watered as needed using a drip irrigation system with no fertilization. All pots received the same amounts of water and pesticide. Excess water drained through holes in the base of the pots.

Measurements and statistical analyses

Before planting, roots of the trees were cut to a length of 20 cm. Initial height, trunk diameter and fresh biomass per individual were recorded. Dead individuals were replaced 5 weeks after planting and again in autumn 2006 (30 weeks after planting). Height and trunk diameter were measured twice during the experiment (after 20 weeks and at harvest). Likewise, the leaf area index (LAI) was measured in the first and second growing season (after 14 and 59 weeks) with a LAI meter (LAI-2000, LI-COR Biosciences). One measurement above and two measurements below the canopy were taken in each pot with three quarters of the "fish eye" optical sensor covered to avoid side effects of neighbouring pots. All trees were harvested after 71 weeks at the end of their second growing period, separated into shoots and roots, dried at 60°C and weighed. Trees were harvested before their roots filled out the pots completely.

Plant size at harvest (height, trunk diameter, above- and belowground biomass and root/shoot-ratio) and LAI were analysed using mixed-effect models with sequential sums of squares (PROC MIXED in SAS, version 9.1, SAS Institute Inc., Cary, NC, USA). Density, diversity and the density x diversity interaction were tested as fixed factors, whereas block, species composition (nested within diversity) and the density x species composition interaction were considered random. Initial plant size (initial height, trunk diameter or biomass, respectively), replacement

of dead individuals (the number of individuals replaced in each pot in spring and autumn 2006, respectively) and mortality (the number of dead individuals at harvest) were included as covariates in the fixed term of the model.

Recent criticism questions the use of biomass ratios to test biological hypotheses because allocation patterns may change allometrically with plant size (Müller et al. 2000). Therefore, values for root/shoot-ratio were additionally adjusted for total biomass (model as above with total biomass as a covariate). The absolute increase in height and trunk diameter over time of every individual was fitted by a linear relationship using a least-squares regression (R 2.6.2). The slopes of these regressions were then analysed with the mixed-effect model approach (see above).

Different measures were used to compare mixture yields relative to their component monocultures. The additive partitioning method (Loreau and Hector 2001) was applied to the biomass data to partition the net biodiversity effect (NE) on productivity into the complementarity effect (CE) and the selection effect (SE). This method assesses the yield of species mixtures relative to a weighted average of the monoculture yields of all of the component species, under the null hypothesis of identical intra- and interspecific interactions (Loreau and Hector 2001, Hector et al. 2002). This was calculated on a per block and density-level basis. Additionally, the SE was further divided into a dominance effect (DE) and a trait-dependent complementarity effect (TDCE) as proposed by Fox (2005). However, the SE (after Loreau and Hector 2001) almost exclusively reflected the DE, whereas TDCE was negligible. Therefore, only the partitioning of NE into CE and SE is presented. Furthermore, complementarity was assessed in relative terms by calculating the relative yield total (RYT) - the sum of every species' yield in mixture divided by its yield in monoculture - for each species mixture (Harper 1977, Hector 1998). Values of RYT greater than one indicate overyielding (Hector et al. 2002). We further tested for transgressive overyielding (i.e. mixture yields in excess of any component monoculture) following Loreau (1998; $D_{max} > 0$). The different components of the biodiversity effects, RYT and D_{max} of the species mixtures were analysed with similar models as plant growth (see above).

A priori orthogonal contrasts were used to test the hypotheses (i) that plant growth and productivity is lower in monocultures compared to all species mixtures and (ii) that this effect depends on density (monocultures vs. mixtures x density). Additionally, data were reanalysed after excluding all pots with dead trees at harvest (n = 16), but most results did not change qualitatively. Dead trees at harvest (n = 19) were excluded from all analyses.

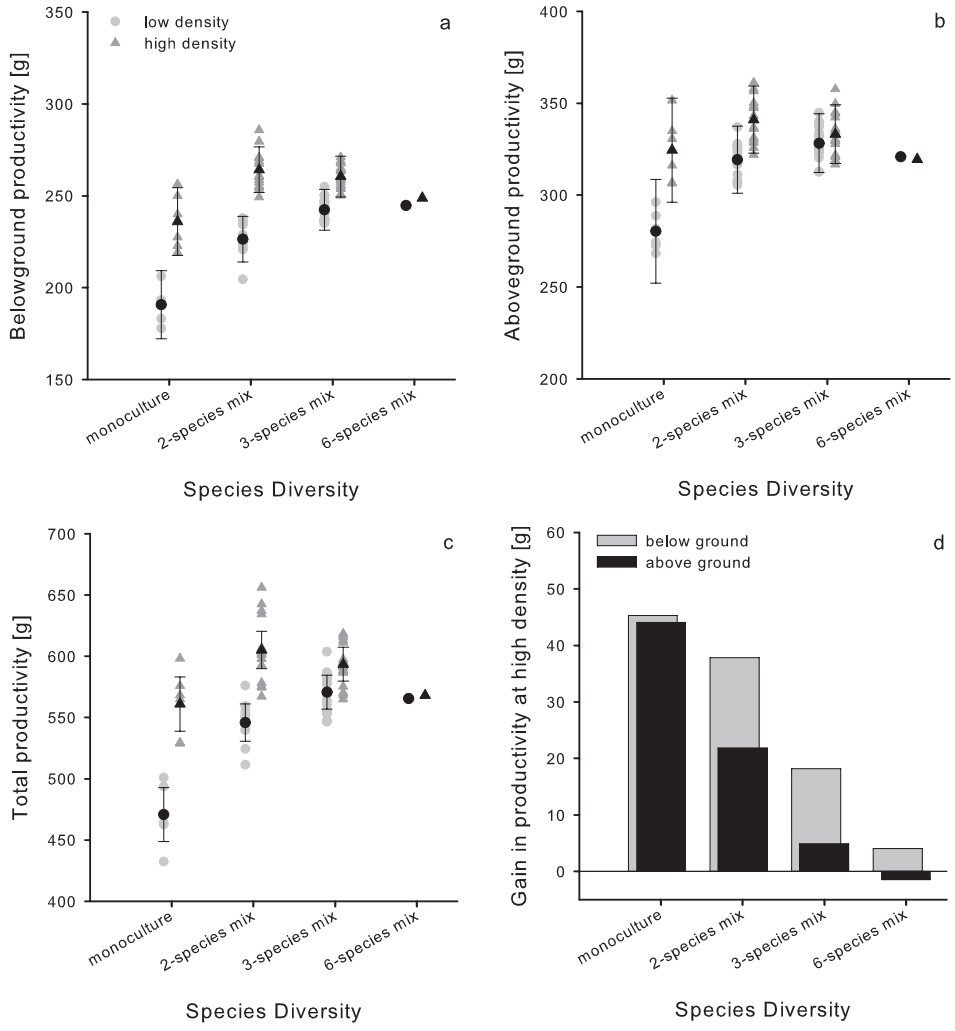

Fig. 1. Effects of density and diversity on the stand (a) belowground, (b) aboveground and (c) total productivity, as well as (d) proportion of productivity gained by doubling the number of trees planted (i.e. differences in productivity at high and low density). Black points (low density) and triangles (high density) are estimated mean productivity ± standard error of different monocultures and species mixtures (light grey points and triangles). For statistical analyses see Table 1.

Table 1. Results of the mixed models (restricted maximum likelihood method) for stand productivity. Each variance component is followed by one standard error and levels of significance were determined from Wald *Z*-tests. The containment method was used to determine the degrees of freedom (d.f.). Levels of significance: $^{(*)}$ $P < 0.1$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. Composition = species composition.

Source of variation	**Belowground**		**Aboveground**		**Total productivity**	
Random effects	**Var**iance **comp**onent	*Z*	Var comp	*Z*	Var comp	*Z*
Block	110 ± 100	1.1	80 ± 80	1.0	249 ± 238	1.1
Composition	1375 ± 379	3.6***	3852 ± 981	3.9***	684 ± 422	1.6$^{(*)}$
D x Composition	248 ± 117	2.1*	416 ± 183	2.3*	942 ± 425	2.2*
Residual	969 ± 88	11.0***	1449 ± 131	11.1***	3465 ± 312	11.1***
Fixed effects	d.f.	*F*	d.f.	*F*	d.f.	*F*
Initial biomass	1, 245	77.2***	1, 245	289.1***	1, 245	415.6***
Replacement spring	1, 245	9.7**	1, 245	9.5**	1, 245	15.6***
Replacement autumn	1, 245	4.2*	1, 245	0.4	1, 245	1.7
Mortality	1, 245	3.3$^{(*)}$	1, 245	0.2	1, 245	0.1
Density	1, 38	26.8***	1, 38	5.5*	1, 38	20.0***
Diversity	3, 38	1.4	3, 38	0.3	3, 38	4.4**
D x Div	3, 38	1.9	3, 38	1.7	3, 38	2.5$^{(*)}$

Results

Effects of tree density and diversity on stand productivity and leaf area index

Stand productivity increased with increasing levels of diversity, with the main difference being between monocultures and species mixtures (Table 1, Fig. 1). On average, total productivity was increased by 11 % in mixed compared to monospecific stands (contrast monocultures vs. mixtures: mixed model, $F_{1,38} = 7.48$, $P = 0.009$, Fig. 1c). However, this positive relationship was much more pronounced at low density (19 % average increase in productivity in mixed stands compared to only 5 % at high density; Table 1, contrast monocultures vs. mixtures x density:

mixed model, $F_{1,38} = 3.61$, $P = 0.065$, Fig. 1c). When analysed separately, tree diversity had no significant effect on above- or belowground productivity (Table 1, Fig. 1a, b). However, belowground productivity tended to increase with increasing diversity, but at low density only (diversity effect at low density: mixed model, $F_{3,38} = 2.26$, $P = 0.097$, Fig. 1a). Above ground this tendency was much weaker (Fig. 1b).

Higher planting density also increased stand productivity, although mainly at low diversity (marginal density x diversity interaction, Table 1, Fig. 1d). At the six-species diversity level, pots with six and 12 tree individuals (low and high density, respectively) were equally productive (Fig. 1). In other words, mean productivity per tree in six-species mixtures was halved (above ground by 50 %, below ground 49 %) at high density (Fig. 1). However, density did not affect the mean root/shoot-ratio, even after adjusting for total biomass (mixed model, $F_{1,38} = 0.06$ and $F_{1,38} = 0.19$, respectively, both $P > 0.1$), nor did diversity (mixed model, $F_{3,38} = 0.04$, adjusted for total biomass: $F_{3,38} = 0.05$, both $P > 0.1$). Within a given diversity level, species composition affected productivity depending on density (Table 1, Fig. 1). This was also true for the mean root/shoot-ratio, also after adjusting for total biomass (mixed model, $Z = 4.23$ and $Z = 4.21$, respectively, both $P < 0.001$).

The LAI in the first growing season was higher in mixed compared to monospecific stands, but at high density only (contrast monocultures vs. mixtures x density: mixed model, $F_{1,38} = 4.26$, $P = 0.046$), resulting in an overall increased LAI at high planting density in mixtures with high compared to low diversity (density x diversity interaction, mixed model, $F_{3,38} = 2.5$, $P = 0.074$, Fig. 2a). A year later, this effect was reversed and LAI decreased in high diversity mixtures at high density, so that LAI was higher at high density only in mixtures with low diversity (density x diversity interaction, mixed model, $F_{3,38} = 3.07$, $P = 0.039$, Fig. 2b). In both years, the LAI varied with species composition (mixed model, 2006: $Z = 2.25$, $P = 0.012$, 2007: $Z = 3.59$, $P < 0.001$). Nevertheless, variation among monocultures and species mixtures was smaller in the second compared to the first year (Fig. 2).

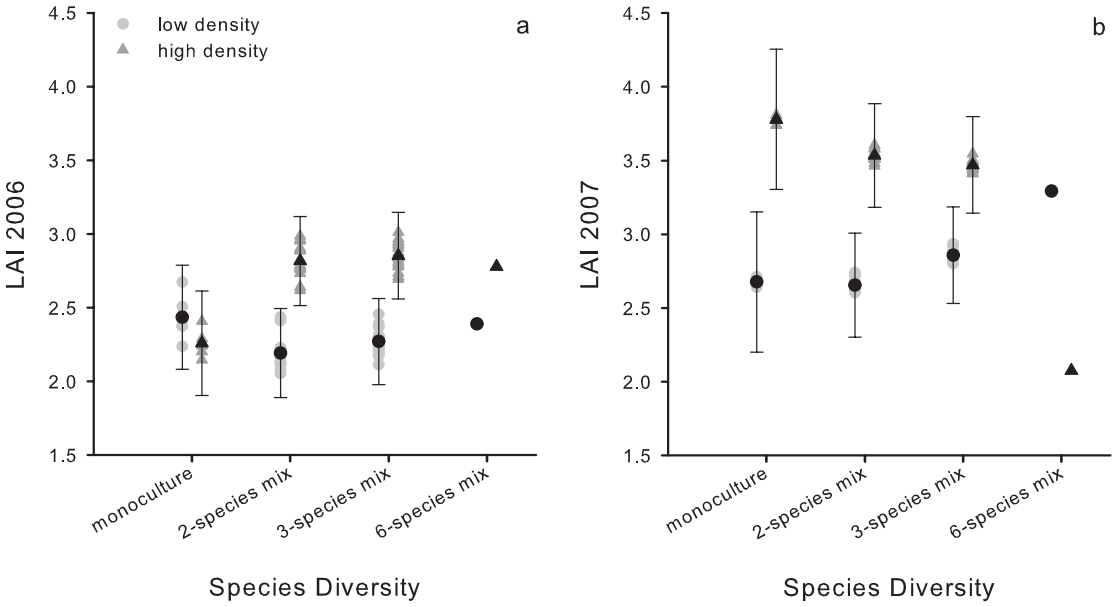

Fig. 2. Effects of density and diversity on the leaf area index (LAI) measured in (a) the first and (b) second growing season. Black points (low density) and triangles (high density) are estimated mean LAI ± standard error of different monocultures and species mixtures (light grey points and triangles). For statistical analyses see text.

Biodiversity effects and relative yield total

The net biodiversity effect (NE) on above- and belowground productivity, and its components the complementarity effect (CE) and the selection effect (SE), were significantly positive overall, with the exception of SE on aboveground productivity (Appendix 1, 2). All three effects on above- and belowground productivity were reduced at high density, whereas diversity had no effect (Appendix 1, 2, Fig. 3). Although not significant, the NE on belowground productivity tended to be positively related to diversity, based on the increase of CE, but at low density only (Fig. 3). This tendency was not found above ground (Fig. 3). At high density, biodiversity effects tended to decrease with increasing diversity and values for NE and SE on aboveground productivity even became negative (Fig. 3). Despite the seemingly high variation in biodiversity effects between different species mixtures, particularly above ground, species composition only significantly affected values of the selection effect (Appendix 1, 2).

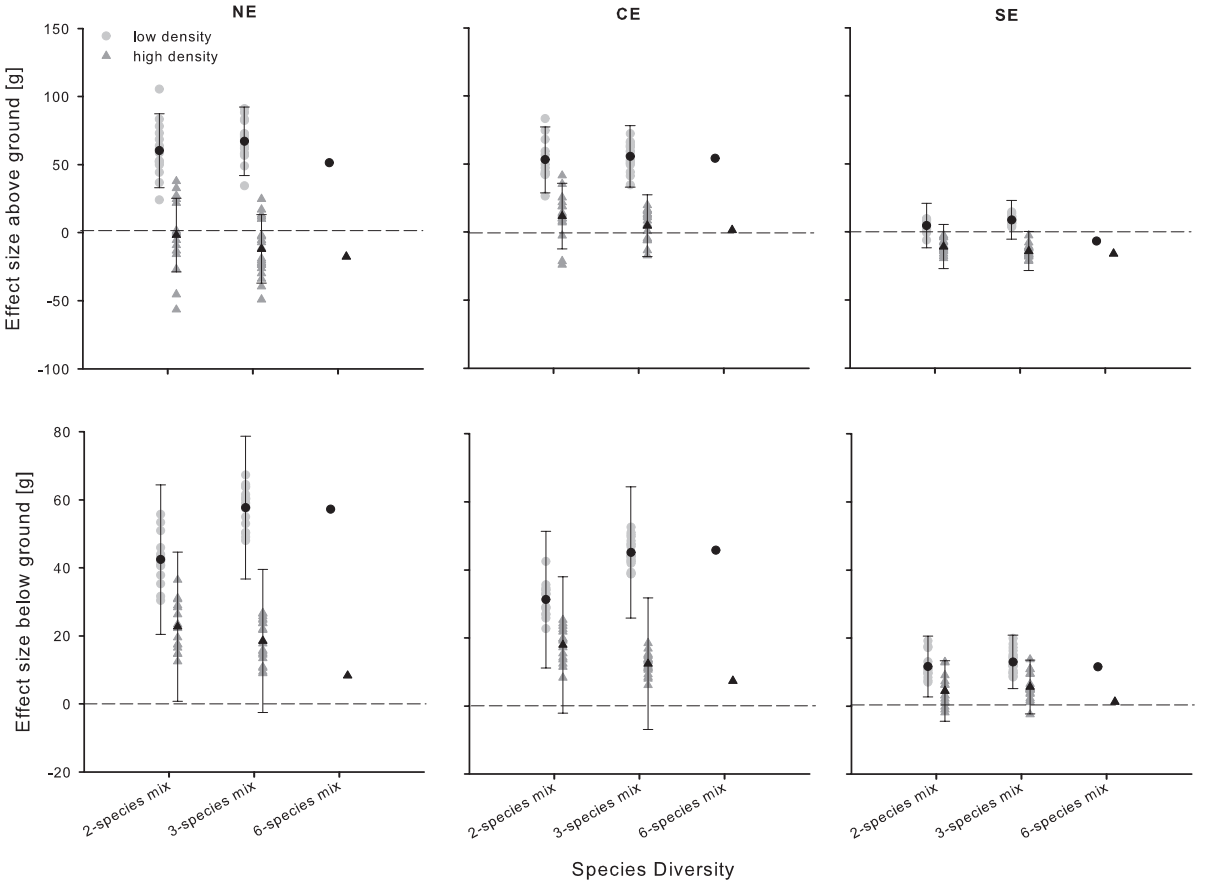

Fig. 3. Effects of density and diversity on the biodiversity effects (NE = CE + SE) for aboveground (top three panels) and belowground productivity (bottom three panels). Black points (low density) and triangles (high density) are estimated mean effect size on productivity ± 95 % confidence intervals of different species mixtures (light grey points and triangles). For statistical analyses see Appendix 1 and 2.

Overyielding was detected for most mixtures, as indicated by values of relative yield totals (RYT) of above- and belowground productivity significantly greater than one (Appendix 1, 2), supporting the results for CE (see above, Fig. 3). Both above and below ground the RYT was higher at low density, whereas diversity had no effect (Appendix 1, 2, Fig. 4). Overyielding above ground was transgressive at low density in 47 % of the two-species mixtures, but non-transgressive at high density (Fig. 4). Below ground, mixtures were transgressively overyielding at low and non-transgressively overyielding at high density (Fig. 4). Transgressive overyielding (i.e. D_{max}) above ground declined with increasing diversity (mixed model, $F_{2,33} = 4.95$, $P = 0.013$, Fig. 4). At high density, the same pattern could be found for RYT above and below

ground and for transgressive overyielding below ground (Fig. 4). The effect, however, was not significant (Appendix 1, 2, mixed model, $F_{2,33} = 0.94$, $P > 0.1$).

Tree growth

Average tree size and aboveground growth did not differ among different diversity levels (mixed model, height: $F_{3,38} = 0.23$, trunk diameter: $F_{3,38} = 0.12$, height increase over time: $F_{3,38} = 0.1$, diameter increase over time: $F_{3,38} = 0.05$, all $P > 0.1$). Only trunk diameter and its increase over time tended to increase with increasing diversity but at low density only (mixed model, density x diversity $F_{3,38} = 2.51$, $P = 0.073$ and $F_{3,38} = 2.47$, $P = 0.077$, respectively). However, within a given diversity level different monocultures and species mixtures varied considerably in all variables describing size and growth above ground (mixed model, height: $Z = 3.46$, trunk diameter: $Z = 3.87$, height increase over time: $Z = 4$, diameter increase over time: $Z = 4.02$, all $P < 0.001$).

Discussion

Overall we found a positive effect of tree diversity on total productivity, via increases in below- but not aboveground productivity, in experimental temperate tree communities. This to our knowledge is the first time that effects of tree diversity have been quantified and separately tested for above- and belowground productivity. However, our results contrast those from temperate forest plantations, which show positive mixture-effects on aboveground productivity (e.g. Assmann 1970, Knoke et al. 2005, Pretzsch 2005, Pretzsch and Schütze 2008). Many of these silvicultural experiments are, however, only partially suitable to address biodiversity ecosystem functioning issues, because they are mostly limited to two-species mixtures of economically important species and particular varieties selected for high productivity (Kelty et al. 1992, Pretzsch 2005, Vila et al. 2005). Observational studies have produced inconsistent results on the biodiversity ecosystem functioning relationship in temperate forests, with some studies reporting a positive effect (Caspersen and Pacala 2001, Vila et al. 2007), and others no

effect (Vila et al. 2003, Szwagrzyk and Gazda 2007). However, these observational studies are difficult to interpret because of the effect of confounding variables, such as density, species composition or site conditions. In contrast, our experimental study has the advantage of explicitly testing the importance of planting density in driving the mechanisms of the relationship between biodiversity and ecosystem functioning.

Positive effects of tree diversity on productivity were most pronounced between monocultures and two-species mixtures. Furthermore, at low density this positive relationship was asymptotic thereafter, whereas it was weaker and more curvilinear at high density, reaching a maximum productivity at the two-species diversity level. In our design the six-species diversity level was only represented by one species mixture, and so results should be interpreted with caution, given that alternative six-species mixtures may yield different results. Complementary resource use and facilitation between species differing in shade-tolerance or rooting patterns has been understood to increase forest productivity (Smith 1986, Cannell et al. 1992, Kelty et al. 1992, Pretzsch 2005, Forrester et al. 2006, Kelty 2006). This is confirmed by our study showing positive net diversity effects to be mainly explained by complementarity rather than selection effects. In addition, the complementary effect was particularly pronounced below ground. To our knowledge, this is the first time that the contributions of complementarity and selection to net diversity effects have been quantified and separately tested for above- and belowground productivity in trees, although with our data we can not elucidate the mechanisms of complementarity or the plant traits involved.

Weakened diversity effects at higher plant densities, as found in our study, have also been observed in experimental grasslands (He et al. 2005). The gain in stand productivity by doubling the number of planted trees diminished in high diversity mixtures. Similarly, the overall reduction in RYT and the complementarity effect when increasing density tended to be more pronounced in high diversity communities. This implies that the complete exploitation of available resources for biomass production is reached faster in high compared to low diversity

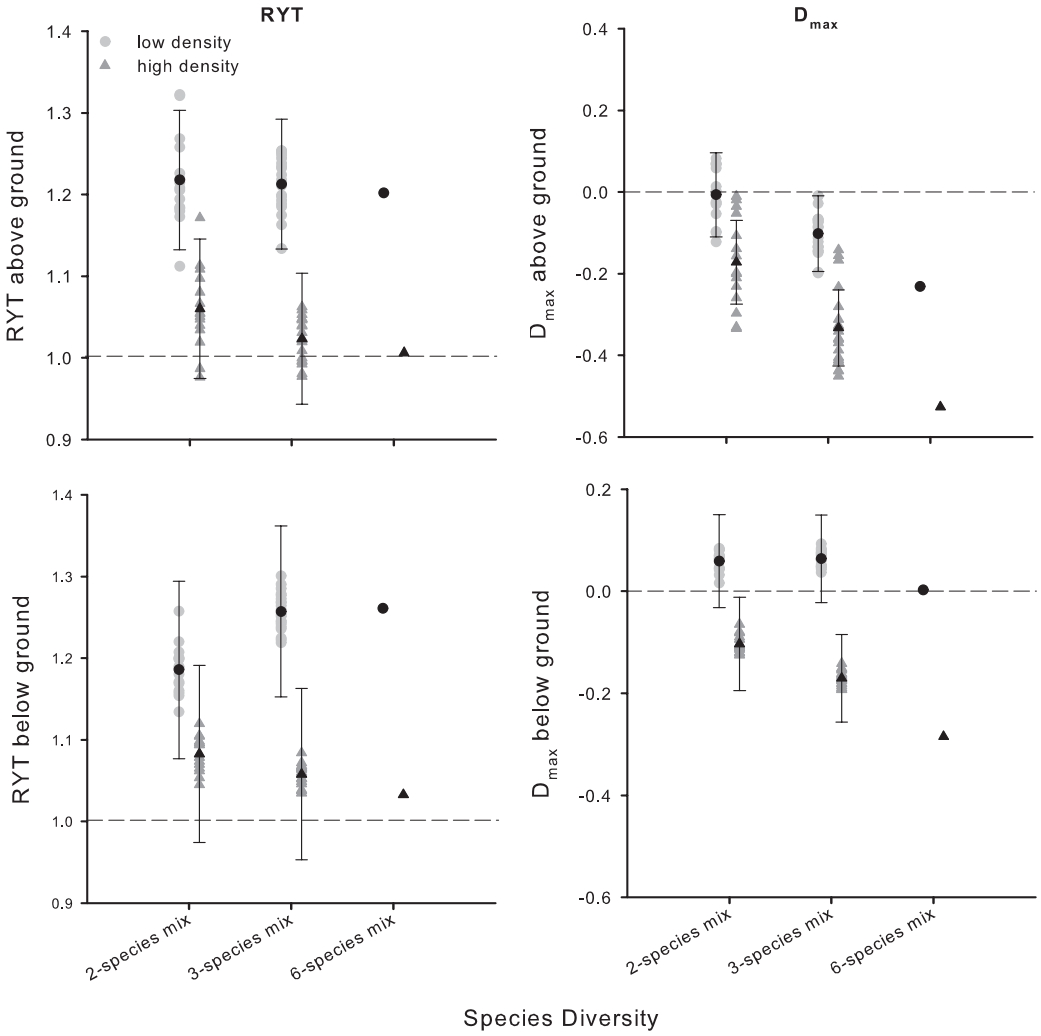

Fig. 4. Effects of density and diversity on the relative yield total (RYT) and transgressive overyielding (D_{max}) above ground (top two panels) and below ground (bottom two panels). Black points (low density) and triangles (high density) are estimated mean RYT and D_{max} ± 95 % confidence intervals of different species mixtures (light grey points and triangles). For statistical analyses see Appendix 1 and 2.

mixtures and monocultures, but also that higher density compensates in part for diversity effects on productivity (as suggested by He et al. 2005 for grasslands). Furthermore, at low density both RYT and complementarity tended to increase with increasing diversity below but not above ground. The limit beyond which further species additions do not increase total niche space utilised by the community (e.g. Dimitrakopoulos and Schmid 2004) may therefore be reached at lower diversity levels above than below ground. This is further supported by

the data on productivity showing density effects to be diminished faster above than below ground with increasing diversity. Nevertheless, allocation patterns, i.e. root/shoot-ratio, were not affected. Decreasing overyielding and complementarity at high density reflects an increase in the predominance of negative or antagonistic interactions due to interference competition - perhaps coupled with effects of biotope space (e.g. Dimitrakopoulos and Schmid 2004) - which even seem to be intensified at higher diversity. Therefore, competitive interactions between tree species probably change with density, which seems plausible but would merit further investigation. Whether non-resource-mediated mechanisms of interference competition occurred and were of relevance is not clear. However, potential indirect effects of natural enemies on the competitive ability of trees can be excluded here, because we treated any infestation with pesticides. Contrary to the study by Polley et al. (2003), the selection effect was more negative at high density. This suggests that selection effects are not driven by the most productive species but rather by species with lower-than-average monoculture yields (perhaps because they can tolerate low resource levels).

Only at high density was the LAI increased in mixtures compared to monocultures in the first growing season. This indicates that positive effects of tree diversity on photosynthetic area may become manifest early in community development if trees interact more intensively at high density. We speculate that greater resource exploitation in mixtures at high density might have led to increased leaf area early in the experiment. A year later there were no longer positive diversity effects and higher density only increased LAI in mixtures with low diversity. Smaller variation in LAI among monocultures and mixtures in the second year indicates that trees changed their branching structure to maximize light exploitation. However, this response occurred in all species independent of community composition and diversity.

Altogether, we demonstrate that planting density is crucial in driving the biodiversity ecosystem functioning relationship and its underlying mechanisms. Neglecting density may therefore in part explain the contradictory results from experimental and observational studies (e.g. Huston 1997), which are often related to abiotic factors and certain species compositions (e.g.

Hooper et al. 2005). For example, initial planting density may have influenced the shape of the relationship between biodiversity and ecosystem functioning found in an experimental tropical tree plantation (Potvin and Gotelli 2008). Therefore, interpretation of results of biodiversity experiments must be made with care and respect to the density at which the communities were planted (see a recent review by Jolliffe 2000 for further discussion). Besides positive effects of tree diversity being significant only on total productivity, we found diversity effects to be more pronounced below rather than above ground. This may explain the failure of some studies which focus on aboveground structures to find a positive biodiversity ecosystem functioning relationship (e.g. Vila et al. 2003, Szwagrzyk and Gazda 2007). However, diversity effects in our tree communities were of a smaller magnitude than those usually observed in grasslands. Compared to grassland species, trees might be more plastic in their ability to use resources for biomass production, depending on their local environment (e.g. competitive neighbourhood). Our findings, however, need to be evaluated under natural conditions and in a long-term perspective, given the long life-cycles of trees as well as potential changes in composition and the contribution of ecological processes and mechanisms over time (Pacala and Tilman 2002, DeClerck et al. 2005, Mokany et al. 2008, Leuschner et al. 2009). For example, effects of tree diversity have been shown to depend greatly on environmental factors, such as climatic variables, soil parameters and other site conditions (Hooper et al. 2005, Körner 2005, Pretzsch 2005, Vila et al. 2005). The substrate used in this experiment was rather nutrient poor and may have therefore enhanced the potential for resource complementarity (von Felten and Schmid 2008).

Despite the caveats of our experiment, we show that tree diversity alters ecosystem properties even at early stages of tree growth. Assuming positive diversity effects to persist or even increase over time, aspects of our study deserve special attention not only from a biodiversity ecosystem functioning perspective but also from silviculture. Increased productivity in mixed compared to monospecific stands and potentially greater resource exploitation through increased complementarity, particularly below ground, may have important implications for

the management of forests for timber production and as carbon sinks (Caspersen and Pacala 2001). We found small positive effects of diversity on tree trunk diameter and its increase over time at low planting density. The accumulation of these differences may translate into higher wood quality and quantity per stem over the life of an individual. Despite a growing body of literature documenting benefits from mixed-species forest plantations (e.g. Pretzsch 2005, Erskine et al. 2006, Forrester et al. 2006, Kelty 2006) mixed-species assemblages are rarely considered in silviculture (less than 1 %), and highly productive monocultures are favoured for timber production (Nichols et al. 2006). Although the magnitude of positive effects of diversity on ecosystem properties very much depends on the species composition, carefully chosen mixtures may increase timber yields while enhancing tree diversity in central European forestry. Nevertheless, we emphasise that tree spacing is a crucial consideration when implementing the concept of mixed stands in forest management.

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Appendix 1. Results of the mixed models (restricted maximum likelihood method) for diversity effects (NE = CE + SE) and relative yield total (RYT) of aboveground productivity. Each variance component is followed by one standard error and levels of significance were determined from Wald *Z*-tests. The containment method was used to determine the degrees of freedom (d.f.). Levels of significance: $^{(*)}$ $P < 0.1$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. Composition = species composition, n.e. = not estimable, CI = confidence intervals.

Source of variation	**NE**		**CE**		**SE**		**RYT**	
	Estimate	$t_{1, 287}$	Estimate	$t_{1, 287}$	Estimate	$t_{1, 287}$	Estimate	$t_{1, 287}$
Overall mean ± 95 % CI	28 ± 7.5	7.3***	31 ± 7.1	8.6***	-3 ± 4.8	-1.2	1.1 ± 0.03	9.9***
Random effects	**Var**iance **comp**onent	*Z*	Var comp	*Z*	Var comp	*Z*	Var comp	*Z*
Block	296 ± 268	1.1	260 ± 243	1.1	10 ± 19	0.5	0.003 ± 0.003	1.1
Composition	177 ± 288	0.6	0	n.e.	572 ± 187	3.1**	< 0.001 ± 0.003	0.04
D x Comp	793 ± 349	2.3*	432 ± 229	1.9*	96 ± 85	1.1	0.005 ± 0.004	1.4$^{(*)}$
Residual	2130 ± 221	9.6***	2661 ± 267	10.0***	905 ± 89	10.2***	0.034 ± 0.003	10.0***
Fixed effects	d.f.	*F*	d.f.	*F*	d.f.	*F*	d.f.	*F*
Initial biomass	1, 209	20.1***	1, 209	6.0*	1, 209	1.7	1, 209	0.4
Replacement spring	1, 209	2.7$^{(*)}$	1, 209	10.3**	1, 209	9.0**	1, 209	8.6**
Replacement autumn	1, 209	1.4	1, 209	1.5	1, 209	0.2	1, 209	1.5
Mortality	1, 209	2.6	1, 209	0.9	1, 209	0.8	1, 209	1.4
Density	1, 33	57.2***	1, 33	29.2***	1, 33	14.4***	1, 33	34.1***
Diversity	2, 33	0.1	2, 33	0.1	2, 33	0.1	2, 33	0.3
D x Div	2, 33	0.5	2, 33	0.2	2, 33	0.5	2, 33	0.2

Appendix 2. Results of the mixed models (restricted maximum likelihood method) for diversity effects (NE = CE + SE) and relative yield total (RYT) of belowground productivity. Each variance component is followed by one standard error and levels of significance were determined from Wald *Z*-tests. The containment method was used to determine the degrees of freedom (d.f.). Levels of significance: $^{(*)}$ $P < 0.1$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. Composition = species composition, n.e. = not estimable, CI = confidence intervals.

Source of variation	**NE**		**CE**		**SE**		**RYT**	
	Estimate	$t_{1, 287}$	Estimate	$t_{1, 287}$	Estimate	$t_{1, 287}$	Estimate	$t_{1, 287}$
Overall mean ± 95 % CI	35.7 ± 5.3	13.2***	27 ± 4.9	10.9***	8.7 ± 2.5	6.9 ***	1.1 ± 0.03	11***
Random effects	**Var**iance **comp**onent	*Z*	Var comp	*Z*	Var comp	*Z*	Var comp	*Z*
Block	300 ± 261	1.2	262 ± 229	1.2	5 ± 7	0.7	0.008 ± 0.007	1.2
Composition	84 ± 107	0.8	42 ± 81	0.5	144 ± 53	2.7**	0	n.e.
D x Comp	156 ± 131	1.2*	91 ± 108	0.8	51 ± 30	1.7*	0.002 ± 0.002	1.0
Residual	1396 ± 138	10.0***	1277 ± 126	10.1***	257 ± 25	10.0***	0.037 ± 0.004	10.2***
Fixed effects	d.f.	*F*	d.f.	*F*	d.f.	*F*	d.f.	*F*
Initial biomass	1, 209	0.7	1, 209	0.1	1, 209	2.9$^{(*)}$	1, 209	1.7
Replacement spring	1, 209	9.4**	1, 209	4.9*	1, 209	3.1$^{(*)}$	1, 209	6.4*
Replacement autumn	1, 209	2.5	1, 209	2.6	1, 209	0.4	1, 209	1.0
Mortality	1, 209	0.5	1, 209	0.1	1, 209	1.2	1, 209	0.01
Density	1, 33	27.4***	1, 33	21.1***	1, 33	6.3*	1, 33	31.1***
Diversity	2, 33	0.4	2, 33	0.3	2, 33	0.1	2, 33	0.4
D x Div	2, 33	1.8	2, 33	2.1	2, 33	0.02	2, 33	1.8

Chapter 2

Root proliferation in response to belowground competition is independent of neighbour identity in tree saplings

Josephine Haase, Daniel Prati

Abstract

Optimal allocation models predict that plants should increase root allocation under competition, even beyond a level that would be optimal if they grew alone. Although this effect has been shown for several herbaceous plants, it has not been tested for trees. In addition it is poorly understood, especially in trees, to what extent root allocation patterns differ depending on the identity of the competitor, despite increasing evidence that plants can react specifically to different neighbouring species. We hypothesised that (1) trees increase allocation to root production as a response to competition, and that (2) this effect is more pronounced for intra- compared with interspecific competition due to potential niche differentiation in the latter case. Pairs of conspecific or heterospecific saplings from six temperate tree species were planted into experimental boxes in which they either shared a common space or where the roots were separated in two compartments of equal size. Additionally, trees of each species were planted alone in a box. As predicted, belowground competition increased root production and root allocation, whereas aboveground growth was not affected. However, contrary to the second hypothesis we did not find that the effect of root separation depended on the identity of the competitor species, thus intra- and interspecific competition caused the same increase in root allocation. Our data show that belowground competition results in increased exploitation of resources independent of the identity of competing species, and that this may affect ecosystem processes such as nutrient leaching and productivity in the long-term.

Key words: allocation, belowground competition, root growth, temperate trees, tragedy of the commons, tree biomass production

Introduction

Competition among plants has long been regarded as an important mechanism of plant coexistence, thereby determining plant diversity and ecosystem functioning (Grime 1979, Tilman 1982, Gurevitch et al. 1992). Whereas many studies have shown how plants actively respond to aboveground competition by changes in allocation or morphology (e.g. Horn 1971), far less is known about their response to belowground competition (Wilson 1988, McPhee and Aarssen 2001). This is especially true for trees and other long-lived perennial plants, despite their enormous economic importance (Casper and Jackson 1997, Coomes and Grubb 2000, Jose et al. 2006). In particular on dry and infertile soils, belowground competition may determine the coexistence of tree species, as well as the productivity and dynamics of forests (Cannell et al. 1992, Kelty et al. 1992, Jose et al. 2006). Furthermore, since up to 50 % of carbon is allocated belowground (e.g. Högberg et al. 2001), understanding root competition may have implications for ecosystem functions such as carbon sequestration (Gleixner et al. 2005, Mund and Schulze 2005).

Plants can respond to belowground competition in several different ways (see Hodge 2009 for an overview), including spatial root segregation (Mahall and Callaway 1992, Gersani et al. 1998, Schenk et al. 1999) and increased root allocation (e.g. Gersani et al. 2001). In a recent game-theoretic model based on optimal allocation theory, Gersani et al. (2001) predicted that plants should increase their allocation to roots in the presence of neighbours with whom they share a common space. The rationale for this is that plants gain an additional, relative advantage over their competitors by exploiting the shared resource space. Whereas the model's predictions have been successfully tested for herbaceous plants (Gersani et al. 2001, Maina et al. 2002, Falik et al. 2003, O'Brien et al. 2005), it has to our knowledge not been applied to trees or other long-lived perennials (but see Bartelheimer et al. 2006 for an example with perennial grassland species). However, testing the occurrence of this mechanism in trees is important because

higher root allocation may result in a more thorough exploitation of soil resources which in turn may have crucial implications for carbon storage, soil erosion and other ecosystem processes (e.g. King 1993). Several studies showed that plants can respond differently depending on the identity of the competitor (e.g. Huber-Sannwald et al. 1996). For instance, Bartelheimer et al. 2006 showed that root proliferation changed from segregation in interspecific competition to aggregation in the case of intraspecific competition. Because conspecific individuals are generally more similar in their niche requirements, competition among them should be more intensive compared with heterospecific individuals (Goldberg and Barton 1992). Thus, any response to competition should be more pronounced under intra- compared with interspecific competition.

In this paper we investigate changes in root allocation in response to intra- and interspecific competitors among saplings of six temperate tree species. These species are dominant and commonly planted trees in Central Europe and we cultivated them as pairs of conspecifics and heterospecifics in experimental boxes. Pot experiments with trees are necessarily restricted to early stages of sapling growth, but competition is likely to be very important in saplings because of high variation in mortality among individuals. In addition, pot experiments allow destructive harvests to quantify root allocation that would be nearly impossible in natural stands. In particular, we hypothesise that:

(1) Root biomass allocation of temperate tree species increases in the presence of belowground competition.

(2) This increase in root biomass under competition is larger with conspecific than with heterospecific competitors.

METHODS

Study System and Experimental Design

To test these hypotheses we cultivated single trees and pairs of trees in either separated or un-separated boxes. We tested six major European forest species, all of which represent important timber species: *Fagus sylvatica* L., *Fraxinus excelsior* L., *Tilia cordata* Mill., *Quercus petraea* (Matt.) Liebl., *Pinus sylvestris* L. and *Picea abies* (L.) Karst.. In April 2006, saplings of these six tree species were planted into experimental boxes (27 cm x 17 cm x 22 cm, L x W x H). Some of the boxes were separated with a plastic wall into two compartments of equal size (13.5 cm x 17 cm x 22 cm, see Fig. 1). Pairs of trees were planted into these boxes so that trees either shared (un-separated treatment) or did not share (separated treatment) the resources while keeping the

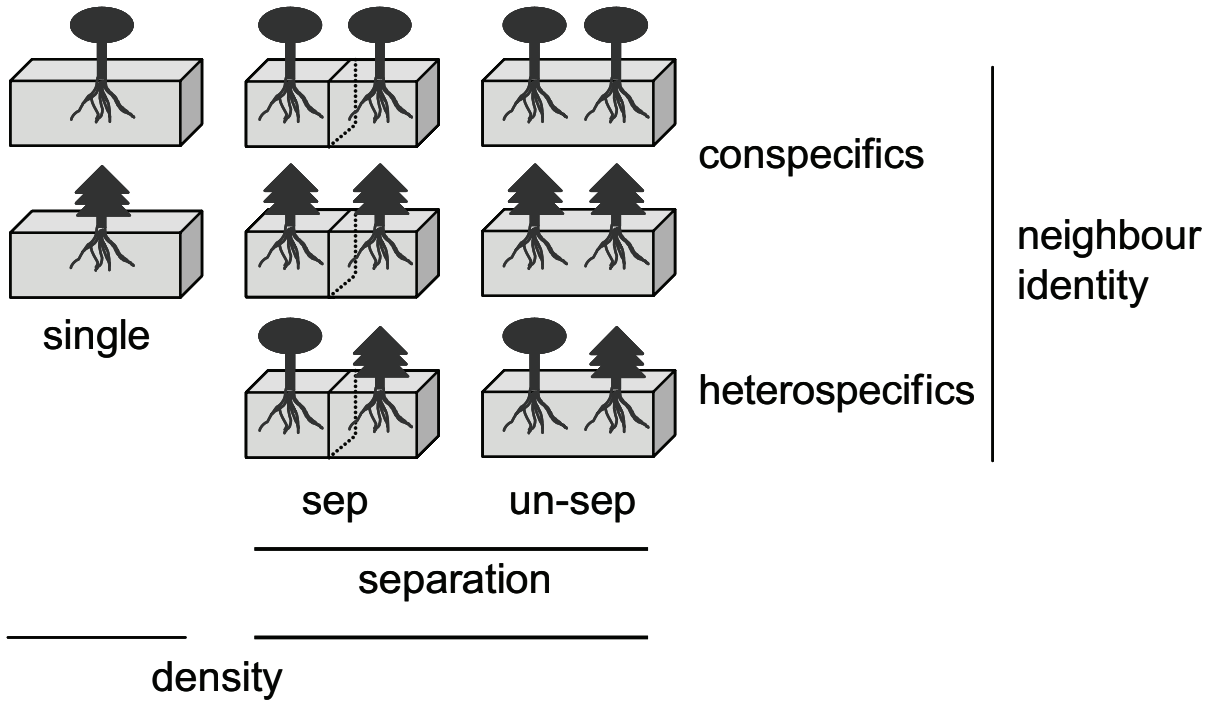

Fig. 1. Experimental design of the experiment. From a species pool of six temperate tree species, individuals were planted alone in a box (single treatment) and as pairs of conspecifics or heterospecifics (all species combinations) in separated and un-separated boxes.

average soil volume per tree constant. In addition, all tree species were planted alone in an un-separated box (hereafter "single treatment", Fig. 1). This design allowed us to test (i) the effects of changes in substrate volume and thus nutrient quantity on growth (single vs. two individuals per box) and (ii) whether trees responded to the presence of neighbouring tree roots (separated vs. un-separated treatment, "hypothesis 1"). Trees in the separated and un-separated treatment were equally spaced and so experienced similar competition aboveground.

All six tree species were planted as pairs of conspecifics in the separated and un-separated treatments (Fig. 1). To test hypothesis 2, all possible combinations of pairs of heterospecifics were planted in the separated and un-separated treatments which allowed us to test whether conspecifics showed a stronger response to the separation treatment than did heterospecifics (Fig. 1, "hypothesis 2"). Each combination of density (single vs. pairs), separation treatment and neighbour identity (con- vs. heterospecifics) was replicated six times in a randomised block design, resulting in a total of 288 pots with 540 trees. Boxes were re-randomized within a block twice during the course of the experiment.

Trees were obtained from a nursery (Fürst Pückler, Zeischa, Germany). The substrate was taken from the upper 10 cm soil horizon of an old fallow site (Kreinitz, Saxony, Germany, 51°23´N, 13°15´E, 95 m a.s.l.) which is currently afforested with the same set of tree species. The soil at that site is characterized as a nutrient poor sandy Cambisol, with a pH of 7.47 and initial nutrient contents of 0.869 % organic carbon, 0.078 % nitrogen and 89.7 mg kg^{-1} plant available P (double lactate-extraction). At planting, species varied in age (one to three years old) and height (15-40 cm), although all individuals of one species were of the same age and approximate height. The initial age and size of trees was similar to that of saplings commonly used for reforestation.

Prior to planting, each box was filled with 2 cm gravel (8-16 mm, Mitteldeutsche Baustoffe, Germany) and 2 cm sand (0-2 mm, Mitteldeutsche Baustoffe, Germany) to ensure drainage, and 6.5 L of sieved (1 cm^2) substrate. The boxes were then placed outdoors in an experimental garden in Bad Lauchstädt, Germany (51°24´N, 11°53´E, 118 m a.s.l.). Over the first growing season,

boxes were shaded (reduction of light by approximately 45 %) and during winter embedded in mulch to prevent frost damage. Infestation of trees by fungal pathogens and herbivores was treated using Ortiva (Syngenta, Germany) and Neudosan (Neudorff, Germany) as necessary, and trees were watered as needed using a drip irrigation system with no fertilization. All boxes received the same irrigation and pest control treatment. Excess water drained through holes in the base of the boxes.

Measurements and statistical analyses

Before planting, roots of the trees were cut to a length of 12 cm and the initial fresh biomass per individual was recorded. Dead individuals were replaced 5 and 27 weeks after planting in spring and autumn 2006, but thereafter boxes containing dead trees (n = 7) were excluded from the analysis. All trees were harvested after 66 weeks, before their roots filled out the boxes completely, separated into shoots and roots, dried at 60°C, and weighed.

Because two trees growing in the same box were not statistically independent, data of individuals were averaged per box prior to analysis. Mean plant size and allocation per box measured as root and shoot biomass, and the root/shoot-ratio, were analysed using mixed-effect models with sequential sums of squares (PROC MIXED in SAS, version 9.1, SAS Institute Inc., Cary, NC, USA). Density (single vs. pairs of trees), separation (separated vs. un-separated, nested within density), neighbour identity (con- vs. heterospecifics, nested within density) and the separation x neighbour identity interaction were tested as fixed factors. Block, species combination (nested within neighbour identity and density) and the neighbour identity x species combination interaction were considered random. Initial biomass and the number of individuals replaced in spring and autumn 2006 were included as covariates in the model. Because allocation patterns may change allometrically with plant size (Müller et al. 2000), root/shoot ratio was additionally analysed with total biomass as a covariate. We also measured plant growth (height and trunk diameter) from repeated measurements, but the results did not differ from shoot biomass and

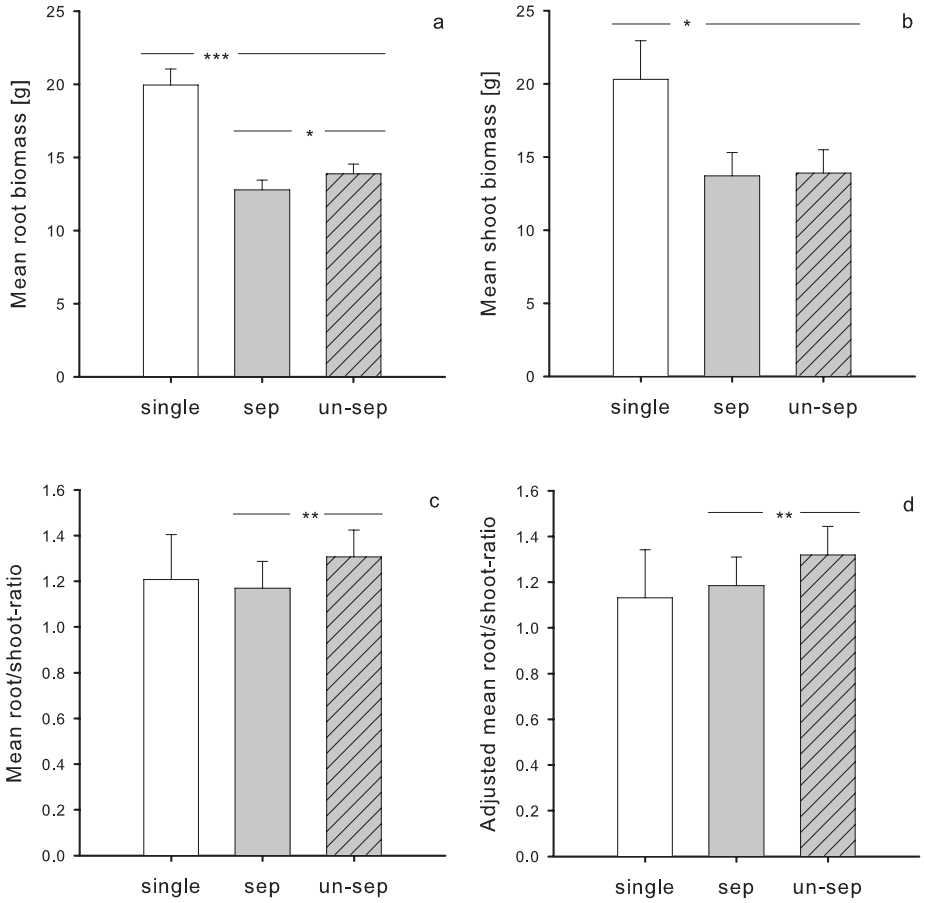

Fig. 2. The effects of density (white vs. grey bars) and belowground separation (open bars: separated; hatched bars: un-separated) on the mean (a) root biomass, (b) shoot biomass, (c) root/shoot-ratio and (d) root/shoot-ratio adjusted for size (final biomass). Values are estimated means ± standard error from the model. Note that standard errors include the variation from the random variables and are therefore not suited to depict significant differences. Horizontal lines above bars therefore indicate significant differences among experimental treatments according to statistical analyses (Table 1). $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

are therefore not presented. Finally, instead of averaging values of individuals within boxes, we performed a split-plot analysis with the variation between individuals within a box used as the error term. But this approach did not qualitatively change the results and we present results from averaged values here.

Table 1. Results of the mixed models (restricted maximum likelihood method) for mean root and shoot biomass and root/shoot ratio. Variance components are followed by one standard error and levels of significance were determined from Wald *Z*-tests. The containment method was used to determine the degrees of freedom (d.f.). Levels of significance: $^{(*)}$ $P < 0.1$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. Final biomass was used as the covariate for the size-adjusted root/shoot-ratio. Combination = species combination, n.e. = not estimable.

Source of variation	**Roots**		**Shoots**		**Root/shoot-ratio**		**Root/shoot-ratio size-adjusted**	
Random effects	**Var**iance **comp**onents	*Z*	Var comp	*Z*	Var comp	*Z*	Var comp	*Z*
Block	0.2 ± 0.3	0.6	0.7 ± 0.6	1.2	0.002 ± 0.002	1.0	0.002 ± 0.002	1.0
Combination	4.7 ± 1.8	2.6**	39.0 ± 11.7	3.3***	0.217 ± 0.065	3.3***	0.248 ± 0.075	3.3***
Sep x Combi	0	n.e.	<0.1	n.e.	0.001 ± 0.003	0.2	<0.001 ± 0.003	0.1
Residual	14.3 ± 1.3	11.0***	11.4 ± 1.0	11.0***	0.062 ± 0.006	10.6***	0.059 ± 0.006	10.6***
Fixed effects	d.f.	*F*	d.f.	*F*	d.f.	*F*	d.f.	*F*
Initial or final biomass	1, 225	118.9***	1, 225	132.9***	1, 225	0.1	1, 225	3.0$^{(*)}$
Replacement spring	1, 225	34.4***	1, 225	20.2***	1, 225	4.1*	1, 225	2.9$^{(*)}$
Replacement autumn	1, 225	2.4	1, 225	2.8$^{(*)}$	1, 225	11.2***	1, 225	12.5***
Density	1, 19	28.9***	1, 19	4.8*	1, 19	<0.1	1, 19	0.3
Separation	1, 19	6.0*	1, 19	0.7	1, 19	14.0**	1, 19	13.9**
Neighbour identity	1, 19	0.1	1, 19	<0.1	1, 19	<0.1	1, 19	<0.1
Sep x Neighbour id	1, 19	0.2	1, 19	0.7	1, 19	0.6	1, 19	1.1

Results

The effect of density and separation on tree growth and allocation

Mean root and shoot biomass per box was reduced by one third (roots 33 %, shoots 32 %) in boxes with two trees (Table 1, Fig. 2a, b), which resulted in a 33 % reduction of total biomass ($F_{1,19} = 24.50$, $P < 0.001$). However, density did not affect the mean root/shoot-ratio (Table 1, Fig. 2c), even after including total biomass as a covariate (Fig. 2d). In support of hypothesis 1, individuals in un-separated boxes produced significantly more root biomass (+ 8 %) than separated trees (Table 1, Fig. 2a), whereas shoot biomass was not affected by the separation treatment (Table 1, Fig. 2b). This resulted in a slightly higher total biomass (+ 5 %) in un-separated than in separated boxes ($F_{1,19} = 4.09$, $P = 0.058$). Root/shoot ratio was higher (+ 12 %) in un-separated than in separated boxes (Table 1, Fig. 2c) and this effect remained when total biomass was included as a covariate (Table 1, Fig. 2d). This indicates that changes in allocation in the separation treatment were independent of plant size.

The effect of neighbour identity on tree growth and allocation

Biomass production and root/shoot ratio varied considerably among the tree species and among different combinations of species (Table 1, Fig. 3). However, they did not differ between pairs of conspecifics and pairs of heterospecifics of different tree species, as indicated by the non-significant neighbour identity effects (Table 1).

Contrary to hypothesis 2, the effect of root separation was not more pronounced under intra- compared with interspecific competition, as indicated by a non-significant separation x neighbour identity interaction (Table 1). In addition, different species combinations did not respond differently to the separation treatment for any of the traits measured (the estimated variance components were either zero or very close to zero; Table 1, Fig. 3).

When analysing the coefficient of variation between the two trees in a box, we found only a

marginally significant increase by the separation treatment ($P > 0.05$ for all traits measured), which suggests that belowground competition caused only a small increase in size asymmetry. Moreover, the separation treatment did not affect the coefficient of variation differently in pairs of conspecifics and heterospecifics (all $P > 0.4$).

Discussion

Across a range of six temperate tree species, we demonstrated that trees exaggerate root production and allocation in response to both intra- and interspecific competitors. Originally, predictions for changes in root allocation in the presence of neighbouring roots were restricted to intra- *versus* interplant competition in annual species (Gersani et al. 2001). Perennial species were expected to show a greater variety of root growth strategies because they compete for nutrients repeatedly with potentially different neighbours (O'Brien et al. 2005, O'Brien and

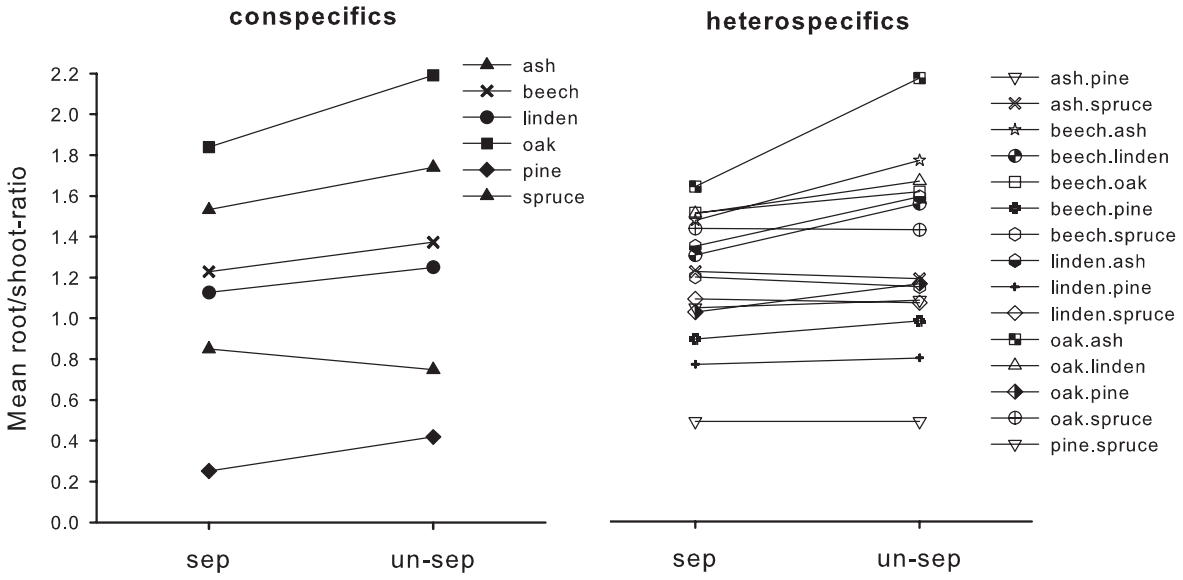

Fig. 3. Effects of belowground separation on the mean root/shoot-ratio in pairs of conspecifics and heterospecifics. Abbreviations: sep = separated treatment, un-sep = un-separated treatment. Values are raw data means and therefore not corrected for the covariates (initial biomass, replacement variables) in the model. For statistical analyses see Table 1.

Brown 2008). However, our results demonstrate that changes in root allocation in response to neighbours among perennials are not fundamentally different from annuals. To our knowledge, this is the first demonstration of this effect in temperate trees.

Root overproduction may be driven by the opportunity to pre-empt resource acquisition of the neighbour, thus increasing belowground competitiveness (e.g. King 1993, Gersani et al. 2001, Bartelheimer et al. 2006). As long as the costs of increased allocation to roots are smaller than the indirect benefit obtained by reducing resource levels for competing individuals, natural selection is expected to favour such a strategy. When all individuals follow the same strategy, this may result in a "tragedy of the commons", in which more roots are produced than would be optimal for individuals growing alone (after Hardin 1968, Gersani et al. 2001). In our study, we did not observe any short-term effects on aboveground growth, neither in pairs of conspecifics nor heterospecifics. A limitation of working with trees as compared with annuals is the lack of data on plant fitness. We thus cannot infer the consequences of higher root allocation for the evolution of populations or the functioning of the whole system. But root overproduction may increase nutrient retention within the system, hence reducing leaching and immobilization of nutrients by other organisms (e.g. Vitousek et al. 1982), and therefore is likely to have consequences for ecosystem functioning (King 1993).

Although it has commonly been assumed that intraspecific is more intense than interspecific competition (Goldberg and Barton 1992), root-overproduction in our experiment was independent of the competitor species' identity. Studies with herbaceous plants or shrubs, however, do indicate an ability to distinguish self from non-self roots, perhaps mediated by physiological coordination among roots of the same plant (Falik et al. 2003, 2006, Gruntman and Novoplansky 2004) or by root exudates (e.g. Mahall and Callaway 1992, Bais et al. 2004, Perry et al. 2005). The absence of a competitor-specific response in our experiment may be explained by an inability of the tree species to identify competitor species. Alternatively, neighbour identification might be unimportant in trees, perhaps because of largely overlapping resource requirements, particularly in early stages of the life cycle. Finally, mycorrhizal infection may

play an important role in tree root recognition. However, in our experiment roots were either not at all or only poorly colonized by mycorrhiza (personal observation). Further studies would be warranted to test the generality of our findings, and to understand why neighbour-recognition in trees is non-specific.

Some authors have argued that increased root production may be the result of reduced self-inhibition (e.g. Falik et al. 2003, Gruntman and Novoplansky 2004, Semchenko et al. 2007) and greater space for proliferation (Falik et al. 2005) rather than the presence of competitors. However, although additional space (independent of nutrients and water) may result in higher root and often higher shoot mass (e.g. McConnaughay and Bazzaz 1991, Semchenko et al. 2007, but see Loh et al. 2003), it should not affect proportional root allocation in the absence of competitors (McConnaughay and Bazzaz 1991). Additionally, plants have been observed to increase root allocation towards competitor roots even if unoccupied space is available (O'Brien et al. 2005, Bartelheimer et al. 2006). In our experiment, proportional root allocation was higher for trees grown under competition than those with exclusive access to the whole substrate volume. Therefore, space *per se* cannot explain the observed patterns. Furthermore, plants experiencing root competition may have lower shoot/root ratios only as an effect of their smaller size (Cahill 2003, Laird and Aarssen 2005). However, root allocation was higher in un-separated compared with separated boxes even after controlling for total biomass, indicating that the presence of a competitor changed allocation independently of changes in tree size. Finally, size asymmetries between pairs of trees may obscure patterns of allocation. Root competition is generally considered to be more symmetric than shoot competition (Schwinning and Weiner 1998), because the spatial distribution of resource-acquiring organs is more important than size *per se* (Schenk 2006). In our experiment we found only a small and marginally significant increase in size asymmetry in the separation treatment, but this effect was independent of the different combinations of plant species. This indicates that size asymmetries cannot explain the observed differences in root allocation in our study.

In conclusion, we found patterns of root allocation as predicted from game-theory on optimal allocation, but no differences between intra- and interspecific competition. More sophisticated studies are required to study root responses to competitors under more natural conditions, e.g. with more than one competitor. In natural forests, roots of individual trees generally extend well beyond their crowns (Kozlowski 1971) and therefore interactions between multiple species occurring over larger distances are likely to be important. Furthermore, despite the difficulties of investigating belowground competition, our experiment showed that a better understanding of root competition may provide valuable insights into resource exploitation. Thus future experiments should focus on the consequences that exploitative competition may have on ecosystem processes such as resource leaching and productivity in tree communities.

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Chapter 3

Soil fauna and litter species composition interactively determine litter decomposition in a temperate system

Josephine Haase, Harald Auge, Stefan Scheu, Daniel Prati

Abstract

Litter diversity affects decomposition through a multitude of direct and indirect pathways. Different litter mixtures may have different effects on decomposer communities whose activity can influence the biodiversity ecosystem functioning relationship. We performed three complementary decomposition trials in a diversity experiment with six temperate tree species to disentangle the different pathways through which litter diversity acts on decomposition processes. Furthermore, we investigated the functional role of soil fauna in decomposition of mixtures differing in litter diversity using coarse and fine meshed litter bags. We hypothesised that litter decomposition rates increase with increasing litter diversity due to non-additive litter mixing effects and more favourable micro-habitat conditions, and that soil fauna determines rates of litter decomposition interactively with litter diversity. Soil fauna, litter species composition and their interaction had large effects on litter decomposition rates. Litter species diversity was not important, although decomposition in mixtures was characterised by synergistic effects in the absence of soil fauna. This suggests a small positive effect of litter diversity on decomposition that may be masked by soil fauna activity and selective feeding preferences. Overall, our data indicate that the direct effects of litter properties and their combination on decomposition are of greater importance than indirect feedback mechanisms, and that soil fauna is an important driver in the biodiversity ecosystem functioning relationship.

Key words: biodiversity, decomposition, ecosystem functioning, litter, decomposer fauna, litter mixtures, trees

Introduction

Leaf litter decomposition is a fundamental ecosystem process, critical for nutrient cycling and energy flow and thereby controlling plant growth as well as community dynamics and structure (e.g. Swift et al. 1979, Wardle 2002, Bardgett 2005). Numerous interacting factors drive litter decomposition, including the physicochemical environment, the quantity and quality of the litter, and the composition of the decomposer community (Berg et al. 1993, Couteaux et al. 1995, Coleman and Crossley 1996, Cadish and Giller 1997). However, most of our understanding of decomposition is derived from studies with litter from single plant species and only recently has research accounted for potential interactions among litter species in mixture, demonstrating that non-additive effects prevail (reviewed by Gartner and Cardon 2004). These non-additive effects can be antagonistic, when decomposition of mixtures is slower than predicted from monocultures of component species (e.g. McArthur et al. 1994), or synergistic when it is faster (e.g. Salamanca et al. 1998). Proposed mechanisms for this are reviewed by Hättenschwiler et al. (2005) and include (1) nutrient transfer among litter types by fungal hyphae or leaching (e.g. Briones and Ineson 1996, Salamanca et al. 1998), and (2) stimulating or inhibiting effects of specific litter compounds on decomposition. Furthermore, non-additive effects may result from (3) inhibition or stimulation of microorganisms and changes in decomposer activity resulting from alterations in microclimatic conditions, habitat and food diversity, and (4) linked effects resulting from interactions across trophic levels (Hättenschwiler et al. 2005).

Thus plant diversity and species composition can affect decomposition in a multitude of direct and indirect pathways. The quantity and quality as well as physical and structural properties of litter may directly influence decomposition, or may act indirectly via its influence on the microenvironment which the litter creates and/or via its influence on decomposer composition, abundance and activity (Fig. 1). Litter from different plant species varying in structural properties create different microenvironments, for example voluminous layers of

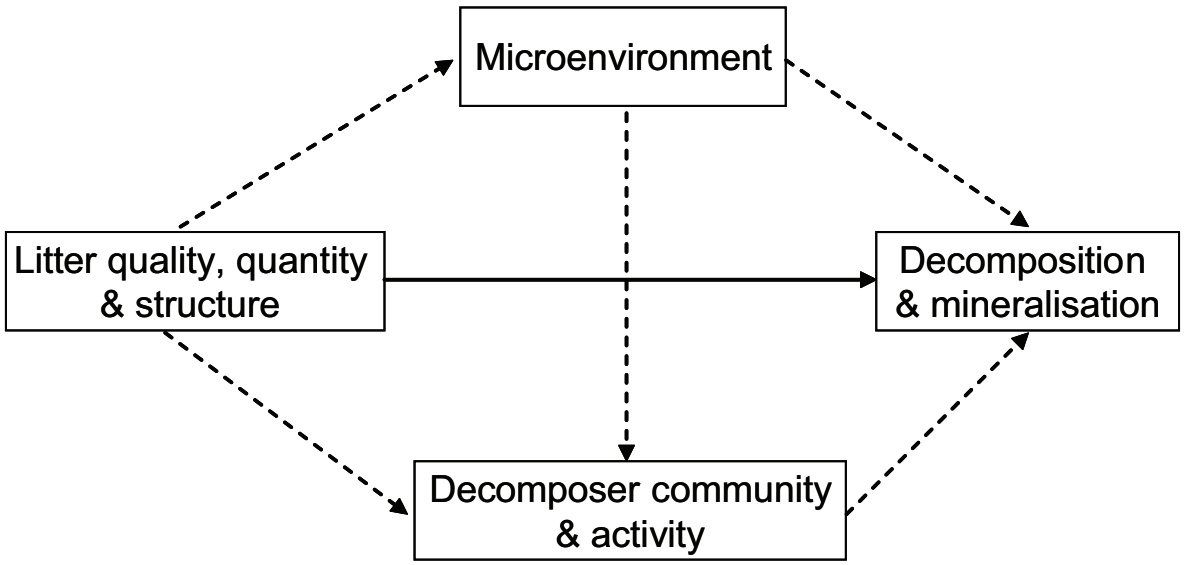

Fig. 1. Direct (solid line) and indirect (dashed lines) pathways of how litter species diversity and composition may affect decomposition processes.

foliose litter versus densely packed needle litter. These types of litter layers vary for instance in their surface-to-volume ratio, the humidity they store, their radiative-energy balance and in the microhabitat structure and niche diversity for decomposers (Hättenschwiler et al. 2005).

Different plant species and different litter mixtures may therefore support specific decomposer communities, whose feeding activity and multitrophic interaction network may influence the biodiversity ecosystem functioning relationship (e.g. Schädler and Brandl 2005). The soil fauna, including oligochaete worms and microarthropods (dominated by Collembola and Acari), largely control the early phase of litter decomposition. Litter displacement, fragmentation and digestion stimulate microbial activity, and the microorganisms' composition, abundance and spatial distribution may be modified by the transport of bacterial and fungal propagules (e.g. Petersen and Luxton 1982, Moore et al. 1988, Maraun and Scheu 1996). The soil fauna thereby facilitates litter decomposition and nutrient mineralization (Scheu and Setälä 2002). However, the relative importance of different players in the soil fauna, and of interactions between the soil fauna and microbes for decomposition processes, can differ from site to site (Seastedt 1984, Heneghan et al. 1998) and among different litter types and mixtures (Schädler

and Brandl 2005). Structurally or chemically more complex litter mixtures may provide more decomposition stages, thus fostering coexistence among decomposers by reducing competition (Hansen and Coleman 1998). However, the relationship between litter diversity and the diversity, abundance and composition of soil fauna remains controversial (e.g. Blair et al. 1990, Kaneko and Salamanca 1999, Wardle and Van der Putten 2002, Wardle et al. 2006), and it has even been argued that some decomposer species are functionally redundant and have no detectable effects on ecosystem functioning (Mikola et al. 2001, Wardle 2002).

The aim of this study was to disentangle the different pathways through which plant diversity acts on decomposition processes, an attempt seldomly made in litter diversity experiments (but see Scherer-Lorenzen 2008 for a grassland example) and to study the functional importance of soil fauna along a diversity gradient. This was done in a recently established diversity experiment with six temperate tree species. In this experiment, plots differing in tree and corresponding litter diversity were established under standardized conditions in the field. We performed three complementary decomposition trials investigating (1) decomposition of a standard material to test for indirect effects of the microenvironment, (2) decomposition of litter mixtures in a common environment to test for direct effects of litter diversity and properties and its interaction with soil fauna, and (3) decomposition in plots of differing species diversity to investigate interactive effects of microenvironment, litter properties and soil fauna. Irrespective of the pathway, our overall aim was to test whether litter diversity does affect decomposition and whether soil fauna activity influences this relationship. More specifically, we addressed the following hypotheses:

(1) Litter decomposition increases with litter diversity, and due to indirect pathways this effect is more pronounced in an environment containing the same litter diversity than in a common environment.

(2) Soil fauna accelerate rates of litter decomposition more strongly at higher diversity levels since litter mixtures may support different soil fauna communities.

Methods

Study site and experimental design

We studied litter decomposition at an experimental site located near Kreinitz (Saxony, Germany, 51°23´N, 13°15´E, 95 m a.s.l.), adjacent to a forest plantation dominated by pine and oak. Mean annual precipitation is 550-600 mm and mean annual temperature 8.4 °C. The soil is a nutrient poor Cambisol, with a pH of 5.5 ± 0.9 (mean ± standard error, 0.01 M $CaCl_2$) and a high sand content of 94 ± 4 % (H.-U. Neue, unpublished data). The site is former arable land, abandoned in the early 1990s.

In 2005, a tree diversity experiment was established on the site to investigate the effects of tree and litter diversity on ecosystem functioning. On an area of 0.75 ha, 98 experimental plots each of 25 m^2 (5 x 5 m) were established, varying in tree species diversity and composition. The species pool contained six temperate tree species: *Fagus sylvatica* L., *Fraxinus excelsior* L., *Tilia cordata* Mill., *Quercus petraea* (Matt.) Liebl., *Pinus sylvestris* L. and *Picea abies* (L.) Karst., all native and common in Central European forests. The experimental plots were randomly assigned to six diversity levels: bare soil (control with no trees), monocultures (of all six species), and all possible species combinations of the two-species (15 compositions), three-species (20 compositions), five-species (six compositions), and the six-species mixture, resulting in 48 species compositions plus one plot without trees. All treatments were replicated twice in two blocks, resulting in 98 plots in total. Trees were planted as two-year old saplings at a density of 1.2 trees/m^2 (= 30 trees per plot) with an equal number of trees per species in the mixtures.

After planting, all plots except the bare soil plots received air-dried leaf litter of the corresponding species composition at a rate of 600 g m^{-2}. The leaf litter was collected from several monospecific

stands of each species in the region and added to the plots each year in late autumn. Litter on each plot was fixed with netting. We therefore deliberately added leaf litter at a rate of a mature forest, while living biomass on the plots corresponded to a young afforestation. Mixtures were comprised of the different litter species in equal amounts, despite the fact that different species may vary in litter production in natural stands. The litter of the tree species selected for the experiment cover a range of decomposition rates, with *F. excelsior* and *T. cordata* having rather fast-decomposing leaf litter, *F. sylvatica* and *Q. petraea* slow-decomposing leaf litter, and *P. sylvestris* and *P. abies* slow-decomposing needles. In summary, this design allowed us to test the effects of tree and corresponding litter diversity on ecosystem functioning while separating the effects of diversity and species composition.

Litter decomposition experiments

Three composition experiments were conducted using litter bags. In the first experiment, we investigated the decomposition rate of all litter compositions used for the field experiment by placing litter bags with the corresponding litter mixtures on the experimental plots. In the second experiment, we used the same set of litter compositions but tested decomposition under standardised conditions in a common environment (i.e. homogeneous patch without a litter layer) that was established next to the experimental plots. In the third experiment, we investigated decomposition of cellulose filter paper as a standard material that we put on all experimental plots, including the bare soil plots. Furthermore, we studied litter decomposition in litter bags of differing mesh size (5 mm and 20 μm) to distinguish the effects of differently-sized decomposers. The 5 mm mesh allowed the access of most groups of soil fauna, whereas the 20 μm size excluded them but allowed access by bacteria, fungal hyphae, small nematodes and protozoa. Cellulose decomposition was investigated in bags of 5 mm mesh only.

We started the three decomposition experiments in February 2007 with a total of 2022 litter bags and collected one third of them at three harvest dates after 75 days, 257 days and 404 days,

respectively. In the first experiment, we tested 48 compositions of litter in the two blocks of the field experiment with two replicates per plot, resulting in 1152 bags (48 compositions x 2 blocks x 3 harvests x 2 mesh sizes x 2 replicates). In the second experiment, we tested the same 48 litter compositions in two blocks in the common environment, but with only one replicate, resulting in 576 bags. In the third experiment, we tested decomposition of cellulose filter paper on all 98 experimental plots, including the bare soil plots, resulting in 294 bags. For the first and third experiment, the litter bags were buried in the litter layer in the centre of each experimental plot, separated from each other by at least 10 cm. For the second experiment, litter bags were placed on bare soil covered with netting.

Freshly fallen leaf litter of the deciduous tree species was collected in monospecific stands in autumn 2006 and air-dried. Coniferous leaf litter was obtained by collecting branches from forest cuttings and air-drying them until needles fell off easily from the stems. To minimize effects of herbivory and pathogens on decomposition, only litter without visible signs of infestation by either was used. Litter bags (16 x 20 cm) were filled with 6 ± 0.2 g of litter with equal amounts of litter per species in the mixtures. To avoid breakage, the litter was moistened with deionised water when filling the bags. For cellulose, 3 ± 0.2 g of filter paper, corresponding to 10 pieces of Whatman number one of 3 x 11.5 cm, was used per bag. After harvesting, the remaining litter and filter paper was cleaned, dried at 60 ºC and weighed to the nearest mg.

A subset of litter bags (n = 120) were retained for further analysis, including fatty acids of microorganisms, soil fauna, and chemical analyses, and so were excluded from the analysis of decomposition. However, results from these analyses are not yet available.

Statistical analyses

Decomposition rate constants (k) were calculated for each litter monoculture and mixture in the experimental plots and the common environment as well as for the filter paper in the experimental plots. This was done by fitting a single exponential decay model to the changes

in mass remaining over time (Olson 1963, Wieder and Lang 1982) as $x_t = x_0 e^{-kt}$, where x_t is the mass remaining at each sampling date, x_0 is initial mass and t is time in years, with the restriction that at time = 0 all of the initial litter mass was present (Wieder and Lang 1982) .

Prior to analysis, decomposition rate constants (k) were log transformed. Decomposition rate constants k of litter and filter paper in the experimental plots and litter in the common environment were analysed using mixed-effect models with sequential sums of squares (SAS, 9.1, SAS Institute Inc., Cary, NC, USA). The models analysing decomposition in the experimental plots and the common environment included mesh size, diversity (five levels) and the mesh size x diversity interaction as fixed factors, whereas block, litter species composition (nested within diversity, 48 levels) and the mesh size x species composition interaction were considered as random factors. Similarly, decomposition rate constants of the filter paper were analysed with diversity (six levels) tested as a fixed factor and block and species composition (nested within diversity, 49 levels) as random factors, excluding k-values < 0 (n = 2).

Furthermore, expected decomposition rate constants of litter mixtures (k_e) were calculated by fitting the exponential decay model to the changes in expected mass remaining over time (Hui and Jackson 2009). The expected mass remaining in mixtures at each sampling date was calculated as the mean of mass remaining of the component litter species. This was done separately for each block and mesh size. This approach accounts for the nonlinear nature of the exponential decay model and prevents overestimation of expected decomposition rates that are usually calculated as the arithmetic mean of decomposition rate constants k of the component litter species (Hui and Jackson 2009). To test for non-additive effects of mixing litter, observed (k_o) and expected decomposition rate constants were compared by calculating the proportional deviation indices $[100 \times (k_o - k_e)/k_e]$ (Wardle et al. 1997) . This measure allows comparisons between different mixtures after removing effects of litter species identity, thus reducing undesirable variations due to different litter species compositions within each diversity-level (Loreau 1998). Proportional deviation indices were then analysed with similar models as decomposition rate constants (see above).

A priori orthogonal contrasts were used to test the hypotheses (1) that decomposition is slower in monocultures compared to all litter mixtures (monocultures vs. mixtures) and (2) that this effect depends on the mesh size (monocultures vs. mixtures x mesh size). In the case of cellulose decomposition, we tested the hypothesis that decomposition is faster in all experimental plots with trees and litter compared to the bare soil plots (no trees or litter). In addition, analyses were performed using the proportions of initial mass remaining at each sampling date (arcsine square-root transformed) instead of k and including sampling date as a factor in the model. However, results did not change qualitatively and are therefore not presented here. Because, needles of *P. abies* may potentially drop from litter bags built of 5 mm mesh, thus affecting estimates of decomposition rates, data were reanalysed after excluding (1) all bags built of 5 mm mesh, (2) all bags built of 5 mm mesh containing *P. abies* litter in monoculture or 2-species mixtures, or (3) all bags built of 20 μm mesh as well as all bags built of 5 mm mesh containing *P. abies* litter. But again, results were unaffected by the data set used.

Results

Litter decomposition

Both in the experimental plots of the tree diversity experiment as well as the common environment experiment, litter of monocultures and mixtures decomposed exponentially throughout the considered period, as indicated by the good statistical fit of the exponential decay model with average r^2 values of 0.946 ± 0.007 and 0.957 ± 0.005 (mean ± standard error for the plots and the common environment, respectively). The same was true for cellulose decomposition in the experimental plots (r^2 = 0.756 ± 0.022).

Effects of mesh size and diversity on litter decomposition

Litter decomposition was overall faster in coarse than in fine meshed bags, both in the experimental plots and the common environment (Table 1, Fig. 2, 3), indicating that access and

Table 1. Result of mixed models (restricted maximum likelihood method) for litter decomposition rate constants (k [a^{-1}]) of the cellulose filter paper and litter bags in the experimental plots as well as litter bags in the common environment. Each variance component is followed by one standard error and levels of significance were determined from Wald *Z*-tests. The containment method was used to determine the degrees of freedom (d.f.). Levels of significance: $^{(*)}$ $P <$ 0.1, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. Composition = species composition.

	Filter paper		**Experimental plots**		**Common environment**	
Source of variation						
Random effects	**Var**iance **comp**onent	*Z*	Var comp	*Z*	Var comp	*Z*
Block	0.014 ± 0.027	0.5	0.0012 ± 0.0019	0.7	0.0005 ± 0.0008	0.6
Composition	0.006 ± 0.037	0.2	0.0381 ± 0.0101	3.8***	0.0125 ± 0.0043	2.9**
Mesh size x Comp			0.0107 ± 0.0035	3.1**	0.0085 ± 0.0029	3.0**
Residual	0.233 ± 0.049	4.8***	0.0131 ± 0.0014	9.3***	0.0069 ± 0.0011	6.2***
Fixed effects	d.f.	*F*	d.f.	*F*	d.f.	*F*
Mesh size			1, 43	260.9***	1, 43	304.9***
Diversity	5, 43	1.2	4, 43	0.2	4, 43	0.3
Mesh size x Div			4, 43	0.1	4, 43	0.4

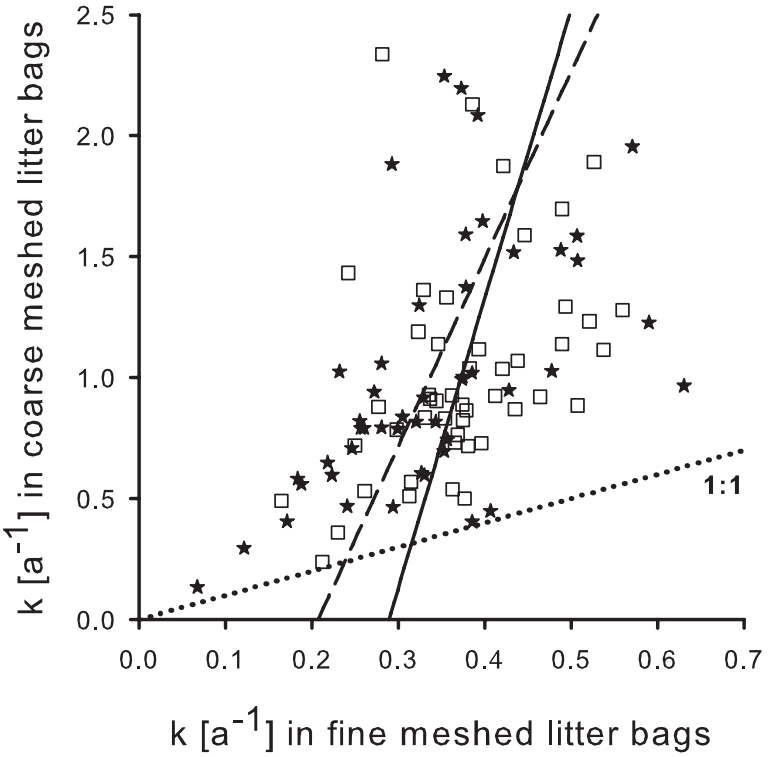

Fig. 2. Relationship (major axis regression) between decomposition rate constants (k) in coarse and fine meshed litter bags in the experimental plots (stars and dashed line) and the common environment (squares and solid line). Every symbol refers to the mean of a specific litter species composition across all blocks (two replicates). The 1:1 line is shown by the dotted line. Both slopes are significantly steeper than one (95 % confidence intervals). For statistical analyses see text.

activity of soil fauna increased decomposition. This effect was dependent on the litter species composition in the bags (significant mesh size x species composition interaction) but did not interact with litter species diversity per se (Table 1, Fig. 3). Both in the common environment and the experimental plots, decomposition rate constants of the litter species compositions were positively correlated between the different mesh sizes (Fig. 2). This indicates that palatability of litter for soil meso- and macrofauna is similar to that for microfauna. Both slopes of the regression lines were significantly steeper than one (Fig. 2), suggesting an increasing importance of decomposer fauna with increasing palatability of litter. Furthermore, the relationship was stronger in the experimental plots than in the common environment ($r^2 = 0.305$, $P < 0.001$ and $r^2 = 0.161$, $P = 0.005$ for the experimental plots and the common environment, respectively, Fig. 2).

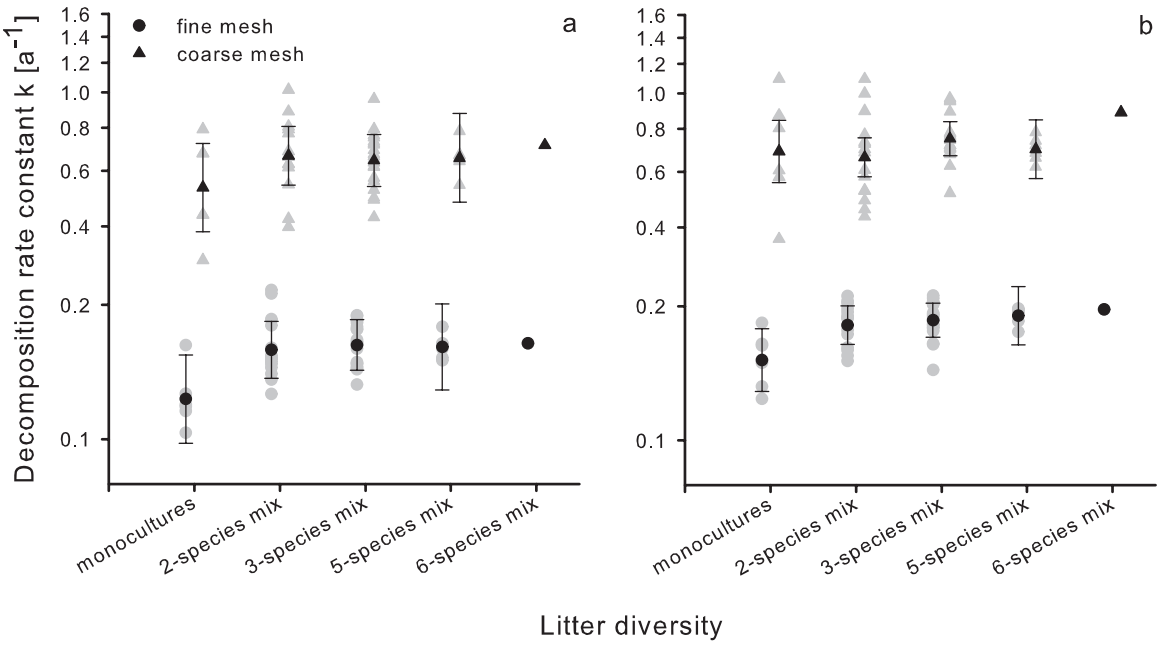

Fig. 3. Effects of mesh size and diversity on decomposition rate constants (k) of (a) litter bags in the experimental plots and (b) in the common environment. Black points (fine meshed bags) and triangles (coarse meshed bags) are estimated mean k ± standard error of different litter monocultures and mixtures (light grey points and triangles). Note that the y-axis is log transformed. For statistical analyses see Table 1.

Whereas litter species composition had a strong effect on decomposition, no effects of litter species diversity were found in the experimental plots and the common environment (Table 1, Fig. 3). However, the variability of litter decomposition rate constants among litter mixtures decreased with increasing litter diversity due to increasing similarity in composition (Fig. 3). This effect occurred at both mesh sizes and in both experiments (experimental plots and common environment). Although litter decomposition rate constants were on average 25 % higher in litter mixtures compared with monocultures in the experimental plots and 15 % in the common environment, this effect was not statistically significant (contrast monocultures vs. mixtures: mixed model, $F_{1,43} = 0.80$, $P = 0.375$ and $F_{1,43} = 0.77$, $P = 0.385$ for the experimental plots and the common environment, respectively, Fig. 3). Furthermore, it is worth noting that the increase in decomposition rate constants in litter mixtures compared with monocultures seemed to be stronger in fine meshed bags in the experimental plots and the common environment (Fig. 3),

even though this was not significant (contrast monocultures vs. mixtures x mesh size: mixed model, $F_{1,43} = 0.24$, $P = 0.624$ and $F_{1,43} = 0.66$, $P = 0.422$ for the experimental plots and the common environment, respectively).

Litter decomposition rate constants of all litter species compositions in the common environment were positively related to those in the experimental plots, irrespective of the mesh size of the litter bags ($r^2 = 0.726$ and $r^2 = 0.758$ coarse and fine mesh, respectively, both $P < 0.001$, Fig. 4). Only in fine meshed bags was litter decomposition faster in the common environment compared with the experimental plots, but this effect was less pronounced for mixtures with higher decomposition rates (Fig. 4).

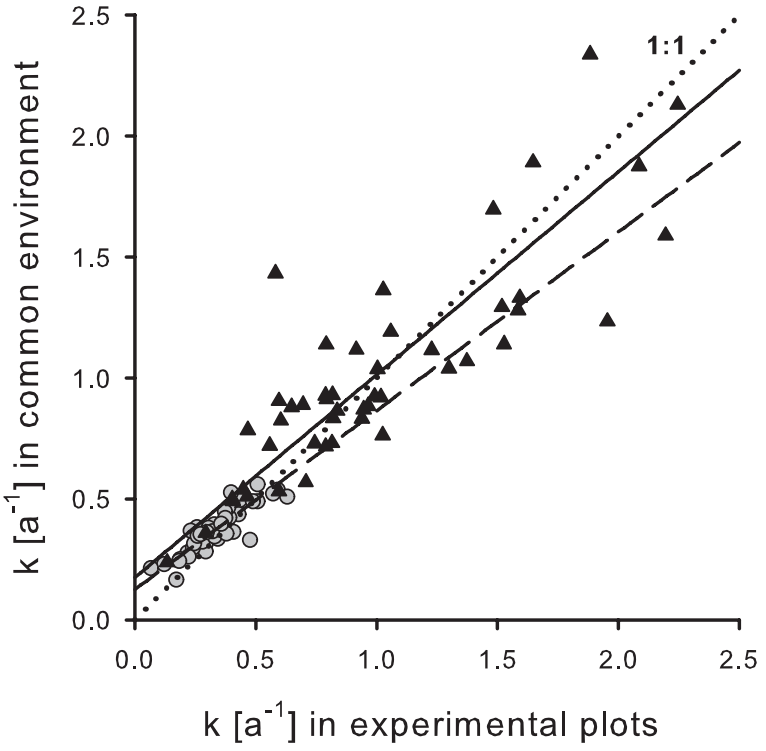

Fig. 4. Relationship (major axis regression) between decomposition rate constants (k) in the experimental plots and the common environment in fine meshed (light grey points and dashed line) and coarse meshed litter bags (black triangles and solid line). Every symbol refers to the mean of a specific litter species composition across all blocks (two replicates). The 1:1 line is shown by the dotted line. Only the slope for the fine meshed bags (dashed line) is significantly flatter than one (95 % confidence intervals). For statistical analyses see text.

Deviations from expected values

Proportional deviation indices between the observed and expected decomposition rate constants were positive overall and greater than zero for both the experimental plots and the common environment (overall mean: 8.71 ± 2.89 % and 6.48 ± 3.83 % mean ± 95 % confidence intervals, experimental plots and common environment, respectively). However, across all litter mixtures neither litter diversity nor species composition had an overall effect on proportional deviations of observed from expected decomposition rate constants in the experimental plots and the common environment (Table 2, Fig. 5). In both experiments, we found synergistic effects on decomposition in fine meshed bags in litter mixtures with low diversity (proportional deviation indices greater than zero, Fig. 5). However, litter mixing resulted in overall additive effects on

Table 2. Result of mixed models (restricted maximum likelihood method) for proportional deviation indices ([%], observed in relation to expected decomposition rate constants k, with expected values calculated based on component litter species) of the litter bags in the experimental plots and the common environment. Each variance component is followed by one standard error and levels of significance were determined from Wald *Z*-tests. The containment method was used to determine the degrees of freedom (d.f.). Levels of significance: $^{(*)}$ $P < 0.1$, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. Composition = species composition, n.e. = not estimable.

	Experimental plots		**Common environment**	
Source of variation	**Var**iance **comp**onent	*Z*	Var comp	*Z*
Random effects				
Block	14.38 ± 26.39	0.5	30.05 ± 51.91	0.6
Composition	0	n.e.	12.69 ± 39.30	0.3
Mesh size x Comp	0	n.e.	0	n.e.
Residual	542.66 ± 49.33	11.0***	558.73 ± 71.83	7.8***
Fixed effects	d.f.	*F*	d.f.	*F*
Mesh size	1, 38	1.8	1, 38	15.7***
Diversity	3, 38	0.3	3, 38	1.1
Mesh size x Div	3, 38	0.1	3, 38	0.7

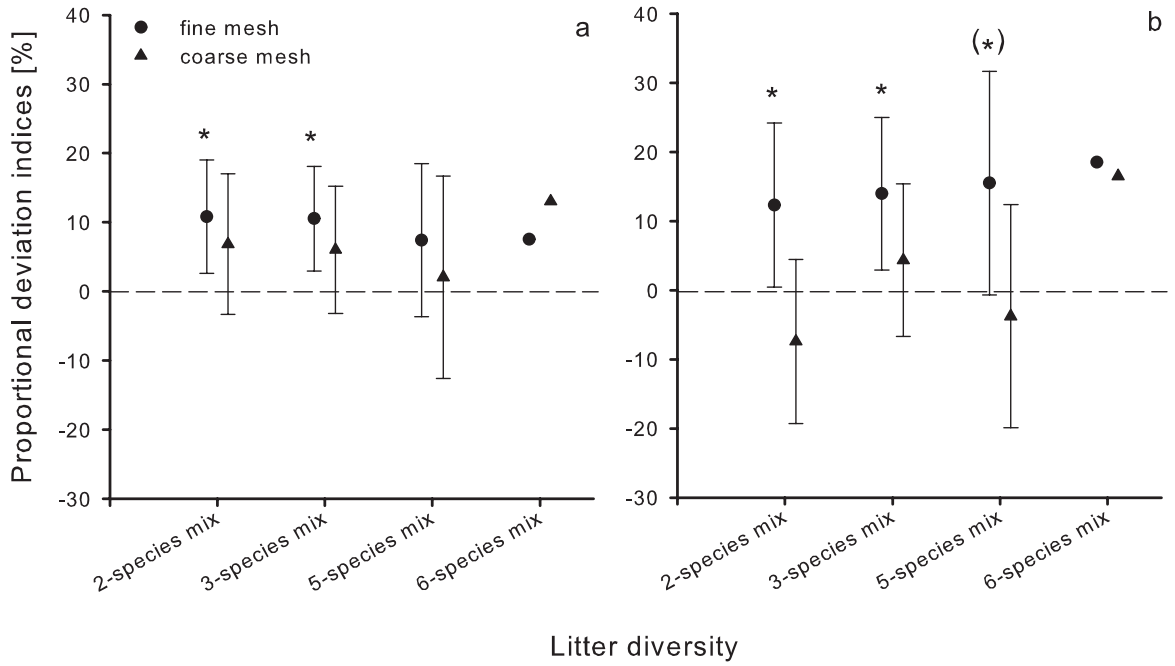

Fig. 5.. Effects of mesh size and diversity on proportional deviation indices (observed in relation to expected decomposition rate constants k, with expected values calculated based on component litter species) of (a) litter bags in the experimental plots and (b) in the common environment. Black points (fine meshed bags) and triangles (coarse meshed bags) are estimated mean deviations ± 95 % confidence intervals. Asterisks indicate significant deviation from zero (no overlap with 95 % confidence intervals). For statistical analyses see Table 2. $^{(*)}$ $P < 0.1$, $^{*}P < 0.05$.

decomposition in coarse meshed bags in the experimental plots and the common environment (Fig. 5).

Effect of litter diversity in experimental plots on decomposition of standard material

Neither diversity nor the composition of litter species in the experimental plots affected cellulose decomposition rate constants (Table 1, Fig. 6). Although not significant, cellulose decomposition rate constants were increased in experimental plots containing trees and litter (on average by 148 %) compared with the bare soil plots (no trees and litter), with the exception of the six-species mixtures (contrast bare soil vs. litter: mixed model, $F_{1,43} = 0.89$, $P = 0.351$, Fig. 6). However, cellulose decomposition was of the same magnitude in the bare soil plots and the six-species mixtures (Fig. 6).

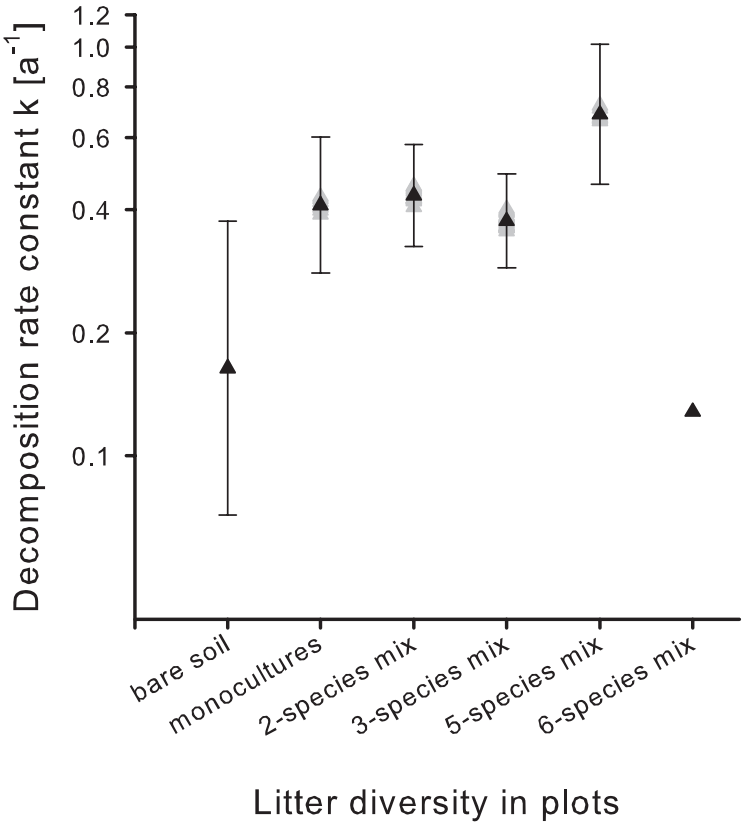

Fig. 6. Effects of diversity on cellulose decomposition rate constants (k) of the filter paper in the experimental plots. Black triangles (coarse meshed bags) are estimated mean k ± standard error of different litter monocultures and mixtures (light grey triangles). Note that the y-axis is log transformed. For statistical analyses see Table 1.

Discussion

Effects of soil fauna on litter decomposition

The presence of soil fauna had the strongest effect on litter decomposition. Soil fauna activity accelerated decomposition irrespective of the microclimatic environment and this depended on litter species composition rather than the number of litter species per se. Similar results were found by Schädler and Brandl (2005), to our knowledge the only other study that has investigated interactive effects of soil fauna and diversity on litter decomposition (but see Milcu et al. 2008 for a different experimental approach). The study by Schädler and Brandl (2005)

was however limited to broadleaf tree species, whereas ours includes two coniferous species that are abundant in Central European forests. Although increased litter decomposition rates in coarse meshed bags should be attributed to soil fauna activity, the potential loss of material as a result of litter fragmentation may have biased litter decomposition measurements and its interpretation (e.g. Schädler and Brandl 2005, Kampichler and Bruckner 2009). Because litter fragmentation is part of the decomposition process (Anderson 1973), we nevertheless consider loss of small litter fragments as a functional role of soil fauna (see also Bradford et al. 2002, Schädler and Brandl 2005). Furthermore, although the potential of *P. abies* litter to be lost from coarse meshed bags was particularly high, this cannot explain the observed patterns as analyses excluding coarse meshed bags containing *P. abies* litter revealed the same results.

The correlation between litter decomposition in coarse and fine meshed bags, both in the experimental plots and the common environment, indicates that there are generally slow and fast decomposing litter monocultures and mixtures (Schädler and Brandl 2005). However, just as Schädler and Brandl (2005), we found soil fauna activity to contribute much more strongly to decomposition of fast compared to slow decomposing litter, suggesting preferences for this type of litter. Differences in decomposition rates have been related to initial litter quality (e.g. Swift et al. 1979, Schädler and Brandl 2005), which might also indirectly affect decomposition by influencing the activity and abundance of soil fauna (Maity and Joy 1999). Overall, the strong dependency of soil fauna activity on species composition as well as the larger contribution of soil fauna to decomposition of fast decomposing litter may indicate that soil fauna activity is driven by food quality rather than litter species diversity per se, which contrasts hypothesis 2. However, with the present data we cannot fully distinguish trophic factors from microenvironment and chemical driven litter interactions affecting decomposition and nutrient dynamics.

Effects of diversity and interactions with soil fauna on litter decomposition

As well as these possible indirect effects through the soil fauna, litter properties had direct

effects on decomposition rates. In particular species composition strongly affected litter decomposition, although litter species diversity in contrast to our expectations had no overall effect on decomposition of either litter or the cellulose standard material. Our findings are consistent with other studies reporting strong species-specific effects on decomposition (e.g. Wardle et al. 1997, Scherer-Lorenzen 2008), whereas no general relationship between litter diversity and decomposition has emerged yet (e.g. Wardle and Van der Putten 2002, Hättenschwiler et al. 2005). While some studies report decomposition to be increased with increasing litter diversity (e.g. Bardgett and Shine 1999, Hector et al. 2000, Spehn et al. 2005), others show no or idiosyncratic effects (e.g. Blair et al. 1990, Wardle et al. 1997). Variability among different species compositions decreased with increasing diversity, due to an increase in similarity among mixtures (Huston 1997). This mechanism has been argued to increase ecosystem reliability with increasing diversity (Fukami et al. 2001).

Contrary to our hypothesis, we did not find significant interacting effects of litter diversity and soil fauna on decomposition. However, although not statistically significant it is noteworthy that in fine meshed bags there was a slight increase in litter decomposition from monocultures to mixtures. Furthermore, synergistic effects of mixing litter were found in the absence of soil fauna, as indicated by greater decomposition rates in fine meshed bags than predicted from component monocultures. This suggests a positive effect of diversity on decomposition rates. Nutrient transfer by fungal hyphae or leaching is understood to alleviate nutrient limitation to poor-quality litter decomposition, which may explain these synergistic effects (Briones and Ineson 1996, Salamanca et al. 1998, Hättenschwiler et al. 2005). Furthermore, an improved microclimatic or a more diverse habitat in litter mixtures may affect microbial and nematode communities (e.g. Wardle et al. 2006), whose multitrophic interactions may in turn influence decomposition positively. However, these diversity effects were not apparent in the presence of soil fauna, perhaps because they were overridden by the activity and potential selective feeding preferences of soil fauna. Preferential consumption of high quality and presumably microbially conditioned litter in mixtures may lead to the loss of alleviated nutrient limitation

to poor quality litter decomposition, thus diluting diversity effects on decomposition rates.

Plant diversity and composition and their "after life effects" (Findlay et al. 1996) affect decomposition through complex pathways, including direct and indirect effects via the physicochemical environment and feed back mechanisms on the decomposer community. Nonetheless, our data indicate that litter properties or their combination have a larger direct effect on litter decomposition than the indirect feedback mechanisms of tree and litter diversity via the microenvironment. This is further supported by the lack of an indirect effect of litter species composition on cellulose decomposition via the microenvironment or specialised decomposer communities in the litter mixtures. Furthermore, contrary to our expectation litter decomposition was not faster in the experimental plots compared with the common environment (hypothesis 1).

Overall, our data demonstrate that soil fauna and litter species composition, but not litter diversity, are important determinants of litter decomposition in a temperate system. However, small synergistic effects of litter mixing may be masked by soil fauna activity, indicating that diversity effects per se are of minor importance in belowground ecosystem processes such as decomposition. This contrasts Gartner and Cardon (2004) who showed that among the non-additive effects of litter mixing, synergistic outcomes are the most frequently reported. However, often study designs include only a proportion of all possible species combinations by creating mixtures from random draws from the species pool. Given the strong interactive effects of soil fauna activity and species composition on decomposition, a restricted sample of mixtures may lead to spurious diversity effects if low-diversity mixtures also tend to comprise low-quality litter species. Therefore, such studies do not convincingly test the effects of litter diversity (number of species as well as species composition) on decomposition. We hypothesise that complex interactions between soil fauna activity and litter diversity particular with the choice of mixtures in the experimental design may at least partially explain the strong idiosyncratic effects in litter mixing experiments (Chapman et al. 1988, Blair et al. 1990, Wardle et al. 1997, Bardgett and Shine 1999). However, further data, especially on nutrient dynamics during

decomposition, changes in decomposition rates of single species in mixtures and information on the decomposer community, are needed to detect and disentangle mechanisms underlying decomposition in different litter mixtures and its associated decomposer community.

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Chapter 4
Phenotypic variation causes synergistic effects of intraspecific diversity on litter decomposition

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Abstract

Although rarely investigated, intraspecific variation and diversity may directly influence community and ecosystem processes. Using European beech (*Fagus sylvatica* L.) as a model system, we investigated variation in litter quality and decomposition among and within populations, and whether litter quality affects decomposition rates. Furthermore, we tested the effects of intraspecific diversity on litter decomposition, hypothesizing decomposition to be faster in mixtures with a higher intraspecific diversity. Litter was collected from six populations, originating from geographically distinct locations throughout Europe and grown in two common gardens. We demonstrate that specific leaf area, C/N-ratio, total phenolic content and litter decomposition varied greatly among individuals within populations, but only weakly among populations. Litter quality variables were, however, poor predictors of decomposition rates. We observed synergistic responses in litter mixtures, with decomposition rates being accelerated by 17 % in mixtures compared with litter from single individuals. Furthermore decomposition in mixtures in relation to expected values based on the decomposition rates of component individuals was increased by 31 % overall. Our findings demonstrate intraspecific variation and diversity to have considerable effects on a fundamental ecosystem process, and are thus relevant for nutrient cycling, community dynamics and the functioning of forest ecosystems. We therefore contribute to the growing awareness of potential effects of within-species variation and diversity on processes at the community and ecosystem level, emphasizing the need to consider this component in the concept of biodiversity and ecosystem functioning.

Key words: biodiversity, decomposition, ecosystem functioning, *Fagus sylvatica*, intraspecific diversity, litter, litter quality

Introduction

Although intraspecific genetic variation has traditionally been assessed in the context of evolutionary processes at the population level, there is growing awareness that genetic variation in ecological traits may also have extended consequences (in the sense of Dawkins 1982) at the community and even ecosystem level (Whitham et al. 2003, 2006). Furthermore, although often overlooked, intraspecific genetic diversity may have wide-ranging ecological consequences for ecosystem processes and functions (e.g. Whitham et al. 2003, 2006, Crutsinger et al. 2006). It is therefore crucial to assess and understand the extent to which intraspecific variation and diversity influence ecosystem functioning, particularly in the face of widespread anthropogenic reductions in forest genetic diversity (Ledig 1992).

The decomposition of leaf litter is a key ecosystem process, integral for energy flow and nutrient cycling and thereby controlling plant growth (e.g. Swift et al. 1979, Wardle 2002, Bardgett 2005). Studies investigating decomposition of litter from different species have improved our understanding of factors that determine decomposition, such as environmental variables (e.g. temperature, precipitation, soil moisture and chemistry) and litter quality, particularly initial contents of carbon, nitrogen and plant secondary compounds (e.g. Swift et al. 1979, Cadish and Giller 1997). On a finer scale, variation in leaf quality has been shown to exist within single species, which is caused partly by intraspecific genetic variation (Hunter and Hull 1993). Consequently, senescent litter deriving from different genotypes of the same species may vary considerably in quality, resulting in genotype-specific decomposition rates and nutrient release (e.g. Madritch and Hunter 2002, 2005, Madritch et al. 2006). Recent research focuses on potential interactions among litters in mixture and studies mixing litter of different species have demonstrated non-additive effects (antagonistic if slower, synergistic if faster decomposition than predicted from monocultures of component species) in most cases (see Gartner and Cardon 2004 for a review and Hättenschwiler et al. 2005 for potential mechanisms). In contrast, studies

demonstrating effects of intraspecific diversity on decomposition in litter mixtures are scarce (but see e.g. Schweitzer et al. 2005).

While intraspecific variation in decomposition has been investigated either among genetically distinct populations (e.g. Lecerf and Chauvet 2008) or among genotypes within populations (e.g. Madritch and Hunter 2002), investigations of variation at both levels are rare (but see Lecerf and Chauvet 2008). However, large intraspecific variation may occur particularly in widely distributed species, determined by genetic differentiation and/or phenotypic plasticity to environmental conditions (Cordell et al. 1998). Furthermore, whether the effects of intraspecific diversity, usually investigated using distinct genotypes from within a single population, are consistent across different populations is presently unknown. Molecular genetic markers have been a vital tool in describing distributions of genetic variation within and among populations throughout species distribution ranges (e.g. Petit et al. 2002). By contrast, variation in quantitative genetic parameters underlying ecological traits has been little investigated, because it requires provenance trials that are often labour intensive for long lived forest tree species (Latta 2004).

We used European beech (*Fagus sylvatica* L.) as a model species since it is widespread throughout Europe and the most dominant tree species of the potential natural vegetation of Central Europe (Ellenberg 1996), occurring in quasi-monospecific stands (Leuschner et al. 2009). It is a monoecious, wind-pollinated and allogamous species (Schaffalistzky de Muckadell 1955, Merzeau et al. 1994) of great economic and ecological value (von Wühlisch 2007). Extended phenotypes, i.e. the consequences of intraspecific genetic variation at the community and ecosystem level, are likely to be expressed in dominant species such as European beech (Whitham et al. 2003). Recently a silviculture provenance experiment has been established to study phenotypic plasticity and genetic variation in ecological and growth traits of beech, and to quantify the extent of population differentiation and local adaptation in these traits (von Wühlisch 2007). The present study used leaf litter from this silviculture experiment to estimate variation in ecological traits, namely litter quality and decomposition rate, within and among populations of European beech as well as to investigate effects of intraspecific diversity on litter

decomposition. More specifically, we wanted to test the following hypotheses:

(1) Intraspecific variation in litter quality affects rates of decomposition.

(2) Intraspecific variation in litter quality and decomposition rate is smaller within than among populations of European beech.

(3) Litter decomposition is faster in mixtures with a higher intraspecific diversity.

Methods

Litter collection

In autumn 2006, senescent leaf litter of European beech (*Fagus sylvatica* L.) was collected from a silviculture experiment in which individuals from different European source populations (i.e. provenances) were planted in common gardens throughout Europe (see von Wühlisch 2007 for a description). For our experiment, we selected six populations that covered the species' range in Europe: Anguiano, Spain (42°15´N 02°45´W, 950 m a.s.l.), Neuberg-Mürzsteg, Austria (47°45´N 15°28´E, 1050 m a.s.l.), Kladská, Czech Republic (50°02´N 12°37´E, 690 m a.s.l.), Beius-Bihor, Romania (46°41´N 22°16´E, 265 m a.s.l.) and two in Germany: Oderhaus, Lower Saxony (51°40´N 10°50´E, 710 m a.s.l.) and Gransee, Brandenburg (53°00´N 13°10´E, 70 m a.s.l.). Individuals from these populations were cultivated in two of the common gardens: Schädtbek near Kiel, Germany (54°18´N 10°18´E, 40 m a.s.l.) and Gablitz near Vienna, Austria (48°15´N 16°07´E, 350 m a.s.l.).

In each common garden, 50 individuals per population were planted in three plots that were arranged in a randomised block design (for more details on the planting design, see von Wühlisch 2007). Per population and common garden, we randomly chose three individuals in each of the three blocks, resulting in nine trees per population and common garden. From each of the selected

trees we sampled approximately 100 g of litter material as fully senescent leaves directly from the trees (young European beech trees hold their leaves for some weeks after senescence). The litter was individually bagged, air-dried, and stored until the experiment started. To minimize effects of herbivory or pathogens on leaf quality, only leaves without visible signs of infestation were collected. Furthermore, both sun and shade leaves were collected to get a representative sample per individual. At litter collection, trees were 13 years in age.

Determination of litter quality

To quantify initial litter chemistry, a subsample of leaves from each individual was finely ground in a mill, and analysed for total carbon (C) and nitrogen (N) contents using an Elementar Vario EL element analyser (Elementar Analysengeräte GmbH, Hanau, Germany). Total phenolic content was determined using the Folin-Ciocalteu method after acetone extraction (Bärlocher and Graca 2005). To determine the specific leaf area (SLA), a measure of leaf toughness, the projected area of ten differently sized leaves per individual was measured using an area meter (LI-3100, LI-COR Biosciences). Leaves were then dried at 60°C, weighed, and SLA was calculated as the ratio of leaf area to leaf dry mass.

Decomposition experiment

To analyse intraspecific variation in decomposition within and among populations (hypothesis 2), we assessed leaf litter decomposition for each individual from the six populations and two common gardens (n = 54 for litter from Vienna, n = 51 for litter from Kiel). In addition, to analyse the effects of intraspecific diversity (hypothesis 3) we mixed litter from either three or six individuals of the same population (hereafter “within population mixtures”) or from individuals of either three or six different populations (hereafter “among population mixtures”). Mixtures were established separately for the litter from the two common gardens in Vienna and Kiel. Thereby, a diversity gradient with five levels was established (see Fig. 1): (i) single individuals

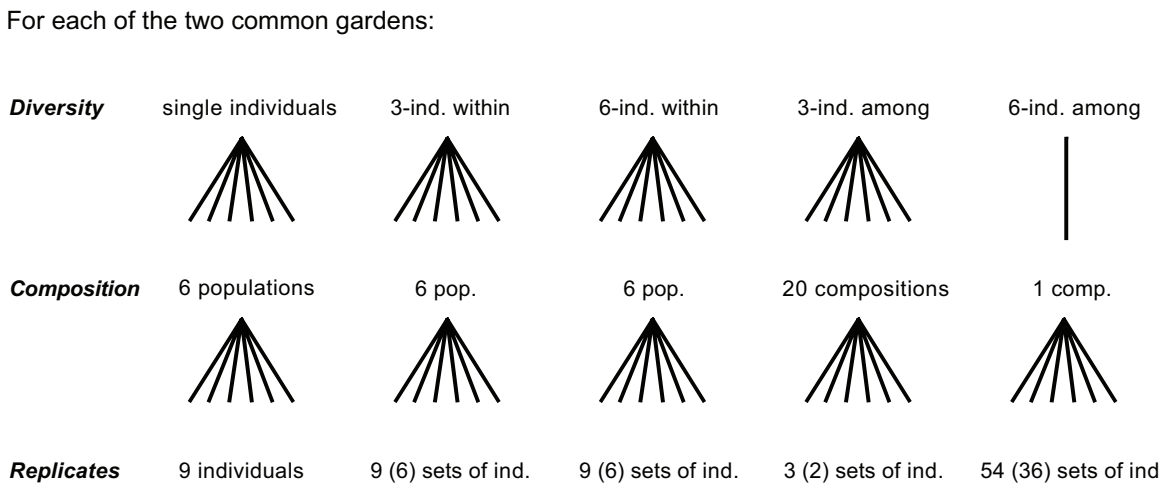

Fig. 1. Experimental design of the litter decomposition experiment. Note that the numbers (in parentheses) refer to the common garden in Kiel (Germany). Within = mixtures of individuals of the same population, among = mixtures of individuals of different populations.

(from the first experiment on intraspecific variation) with the six populations representing different compositions, each replicated using the sampled individuals of each population, (ii) within population mixtures of three or (iii) six individuals (Vienna: n = 54, Kiel: n = 36) with six compositions corresponding to the six populations, each replicated using nine (Vienna) or six (Kiel) different sets of three or six individuals, respectively, (iv) among population mixtures of three individuals (Vienna: n = 60, Kiel: n = 40) with all 20 possible compositions, each replicated using three (Vienna) or two (Kiel) different sets of three individuals, and (v) among population mixtures of six individuals (Vienna: n = 54, Kiel: n = 36) containing always the same composition, replicated using 54 (Vienna) or 36 (Kiel) different sets of six individuals of the six populations. The unique sets of individuals were not replicated (Fig. 1). Litter from each individual tree contributed equally to the different mixtures. However, because of advanced leaf fall in the common garden in Kiel resulting in a shortage of litter from some trees, sample sizes for Kiel were smaller than intended.

Litter boxes (13 x 10 x 6.5 cm), were filled with 3 ± 0.2 g of air-dried litter. The top and bottom of the boxes were sealed with a 4 mm mesh to allow decomposer-access. All mixtures had approximately equal proportions of litter from different individuals (1 g per individual for the

three- and 0.5 g per individual for the six-individual mixtures, respectively). To avoid breakage, the litter was moistened with deionised water when filling the litter boxes.

In late winter 2007, the litter boxes were randomly assigned to three blocks that were placed on bare forest-floor of a mixed stand dominated by *Pinus sylvestris* L., *Quercus petraea* (Matt.) Liebl. and *Quercus rubra* L. near Halle, Germany (51°30´N 11°53´E, 100 m a.s.l.). We deliberately chose a forest without *F. sylvatica* to exclude possible effects of certain beech genotypes or genotype-adapted decomposers already present at a site. Litter boxes were covered with netting to prevent contamination with natural litter fall. In autumn 2008 (after 15 months), the litter boxes were collected and the remaining litter was cleaned with a brush, dried at 60 °C, and weighed.

Statistical analyses

Decomposition rate constants (k) were calculated for litter from each individual and all mixtures as $x_t = x_0\, e^{-kt}$, where x_t is litter mass remaining at harvest, x_0 is initial litter mass and t is time in years (Olson 1963, Wieder and Lang 1982). Litter quality (SLA, total phenolic content, C/N-ratio) of mixtures was calculated as averages from the component litter individuals. To assess the effect of intraspecific variation on litter quality and decomposition rate, mixed-effect models with sequential sums of squares (PROC MIXED in SAS, 9.1, SAS Institute Inc., Cary, NC, USA) were calculated with common garden (Vienna and Kiel) as a fixed factor, and population, block in the common gardens (nested within common garden), the population x common garden interaction and the population x block interaction as random effects. For the decomposition rate constant (k) an additional decomposition-block, referring to the position of the decomposition experiment in the forest, was included as a random term in the model. We used the containment approximation implemented in SAS PROC MIXED to calculate denominator degrees of freedom for the fixed effect (Littell et al. 1996). Satterthwaite's approximation yielded qualitatively similar results which are not presented here.

The effects of intraspecific diversity (i.e. mixing of litter individuals) on decomposition were analysed in two complementary fashions. Firstly, mixed-effect models were used to test the effects of the fixed factors common garden and diversity (five levels, see above) on decomposition rate constants, and decomposition-block and composition (nested within diversity) as random factors. A priori orthogonal contrasts were used to test the hypotheses (i) that decomposition is slower in single individual litter compared with mixtures (single vs. mixtures) and (ii) that decomposition is faster in mixtures of individuals from different populations compared with those from the same population (within vs. among population mixtures). Secondly, the expected decomposition rate constant of litter mixtures (k_e) was calculated by fitting the exponential decay model (see above) to the change in expected mass remaining over time (Hui and Jackson 2009). The expected mass remaining in mixtures was calculated as the mean of mass remaining of the component individuals when decomposing alone. This approach accounts for the nonlinear nature of the exponential decay model and prevents overestimation of expected decomposition rates that are usually calculated as the arithmetic mean of decomposition rate constants k of the component litter individuals (Hui and Jackson 2009). To test for non-additive effects of mixing litter, observed (k_o) and expected decomposition rate constants were compared by calculating the proportional deviation indices [$100 \times (k_o - k_e)/k_e$] (Wardle et al. 1997). This measure allows comparisons between different mixtures after removing effects of litter individual identity, thus reducing undesirable variations due to different litter individual compositions within each diversity level (Loreau 1998). Proportional deviation indices were then analysed with similar models as decomposition rate constants (see above). The influence of litter quality on decomposition rate constants of single individual litter and litter mixtures was tested using linear regression after checking for multicollinearity among litter quality variables, which was negligible. The results were unchanged after adjusting for the variance explained by the experimental design factors (see analysis on intraspecific variation), and are therefore not presented here. In addition, the relationship between litter quality and decomposition were also tested on the population level (n = 6).

Results

Intraspecific variation in litter quality and litter decomposition

Litter differed slightly in total phenolic content and C/N-ratio among populations, whereas no significant differences were found for SLA (Table 1). The lowest values for total phenolic content and C/N-ratio were found in litter of the Spanish population (30.92 ± 15.42 mg g^{-1} total phenolics, 29.24 ± 4.35 C/N, predicted mean ± standard error). In comparison, total phenolic content was twice as high in litter of the Czech population, and C/N-ratios were increased by 26 % in litter from the Oderhaus population in Germany and the Romanian population. In general, variation in litter quality among populations was rather small (SLA: 14 %, phenolics: 21 %, C/N: 28 % of total variation), whereas individuals within populations differed markedly in litter quality (SLA: 74 %, phenolics: 73 %, C/N: 51 % of the total variation was within populations, Table 1).

The two common gardens in which the trees were cultivated had some effect on litter quality, indicating phenotypic plasticity of leaf traits. Averaged over all populations, SLA was higher and the C/N-ratio showed a trend to be higher in litter from Kiel, whereas the total phenolic content did not differ significantly across the common gardens (Table 1, Fig. 2a-c). However, the litter quality of different populations did not differ depending on the common garden where trees were grown (population x common garden interaction not significant, Table 1), suggesting that the genetic contribution to phenotypic variation among populations was consistent across the two environments.

Similar to litter quality, variation in decomposition rate constants (k) was generally higher within than among populations (67 % of total variation within compared with 4 % among populations). Decomposition rate constants were equal across both common gardens and k of different populations did not differ depending on the common garden where trees were grown (Table 1, Fig. 2). However, none of the litter quality variables were significantly related to

Table 1. Result of mixed models (restricted maximum likelihood method) for litter quality and decomposition rate constants (k [a^{-1}]) calculated on the basis of litter individuals. Each variance component is followed by one standard error and levels of significance were determined from Wald *Z*-tests. The containment method was used to determine the degrees of freedom (d.f.). Note that the effect of decomposition-block is only tested on k. Levels of significance: $^{(*)}$ $P < 0.1$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. n.e. = not estimable, C/N = C/N-ratio, SLA = specific leaf area [$cm^2\ g^{-1}$], phenolics = total phenolic content [$mg\ g^{-1}$].

Source of variation	**SLA**		**Phenolics**		**C/N**		**k**	
Random effects	**Var**iance **comp**onent	*Z*	Var comp	*Z*	Var comp	*Z*	Var comp	*Z*
Decomposition-Block							0.0017 ± 0.0019	0.9
Population	164 ± 151	1.1	129 ± 100	1.3$^{(*)}$	11 ± 9	1.3$^{(*)}$	0.0003 ± 0.0005	0.6
Block	13 ± 73	0.2	28 ± 40	0.7	1 ± 2	0.4	0	n.e.
Pop x C g	0	n.e.	0	n.e.	0	n.e.	0.0002 ± 0.0005	0.5
Pop x Block	137 ± 135	1.0	11 ± 54	0.2	8 ± 4	1.8*	0	n.e.
Residual	889 ± 150	5.9***	463 ± 78	5.9***	20 ± 3	5.9***	0.0045 ± 0.0007	6.7***
Fixed effects	d.f.	*F*	d.f.	*F*	d.f.	*F*	d.f.	*F*
Common **g**arden	1, 4	9.7*	1, 4	4.4	1, 4	6.8$^{(*)}$	1, 4	0.8

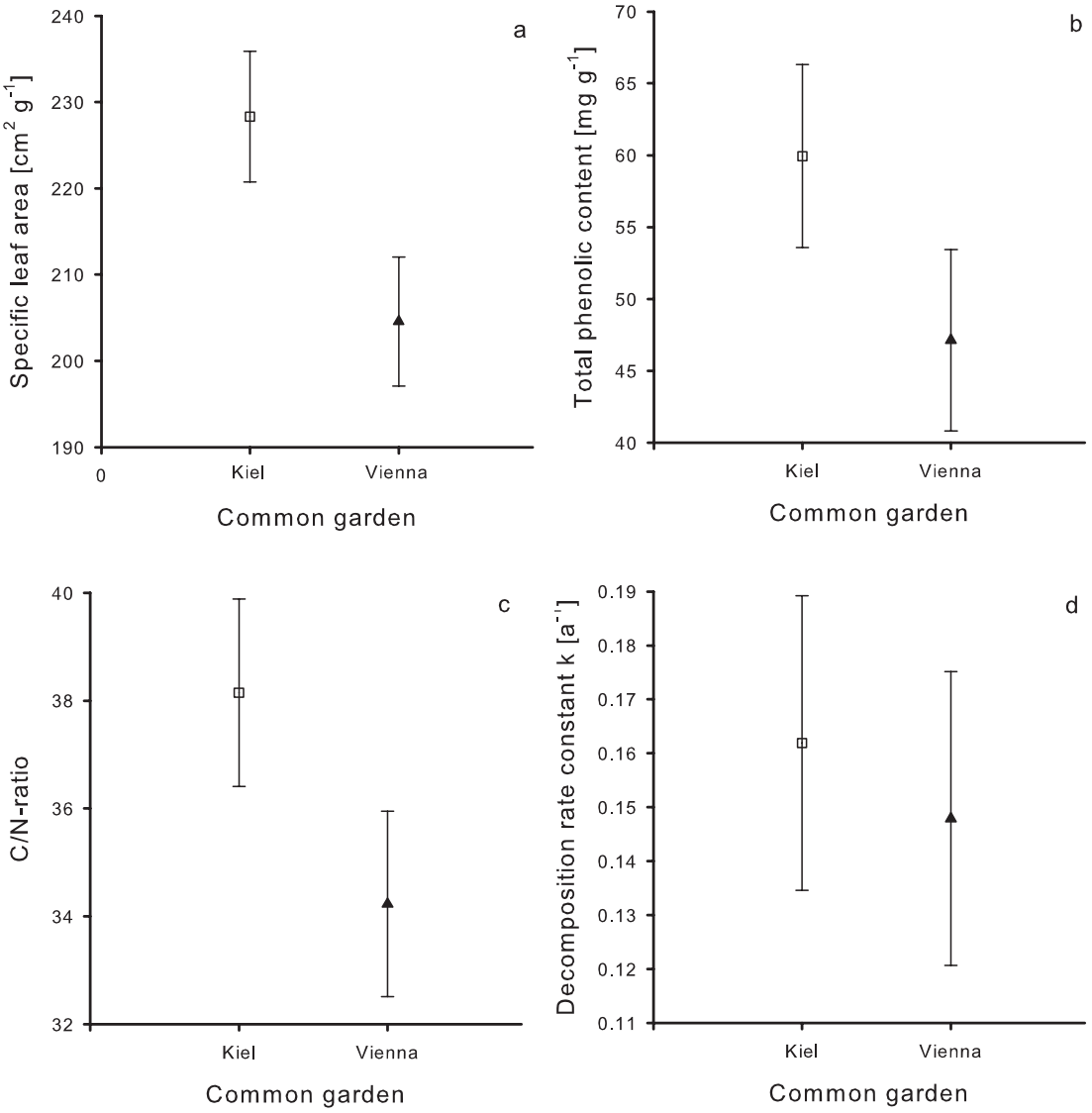

Fig. 2. Litter quality variables (a) SLA, (b) phenolics, (c) C/N-ratio) and (d) decomposition rate constants (k) of litter from the two common gardens. Values (open squares = litter from Kiel, black triangles = litter from Vienna) are estimated means ± standard error. For statistical analyses see Table 1.

decomposition rate constants on the population level (Appendix 1 for results from simple and multiple regressions).

Effects of intraspecific diversity on litter decomposition

Litter decomposition rate constants were increased by on average 17 % in litter mixtures compared with single individual litter (Table 2, Fig. 3a). Furthermore, the decomposition rate constants of the single individuals never exceeded that of the slowest decomposing litter mixture (Fig. 3a). Nevertheless, mixing individuals of the same or different populations had no effect on decomposition rate constants, resulting in an overall weak diversity effect across all levels

Table 2 Result of mixed models (restricted maximum likelihood method) for litter decomposition rate constants (k [a^{-1}]) and proportional deviation indices ([%], observed in relation to expected k, with expected values calculated based on component litter individuals). Each variance component is followed by one standard error and levels of significance were determined from Wald *Z*-tests. The containment method was used to determine the degrees of freedom (d.f.). Levels of significance: $^{(*)}$ $P < 0.1$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Source of variation	**k**		**Proportional deviation indices**	
Random effects	**Var**iance **comp**onent	*Z*	Var comp	*Z*
Decomposition-Block	0.00060 ± 0.00063	1.0	124.9 ± 163.1	0.8
Composition	0.00011 ± 0.00014	0.8	82.2 ± 146.5	0.6
Residual	0.00478 ± 0.00032	14.8***	4679.5 ± 359.4	13.0***
Fixed effects	d.f.	*F*	d.f.	*F*
Common **g**arden	1, 428	5.3*	1, 330	0.3
Diversity	4, 34	2.4$^{(*)}$	3, 29	0.6
Single vs. Mixtures	1, 34	8.1***		
Within vs. among population mixtures	1, 34	0.1	1, 29	<0.1
C g x Div	4, 428	0.9	3, 330	1.7

(Table 2, Fig. 3a). Even though not significant, it is worth noting that decomposition tended to be slower in mixtures with six compared with those with three litter individuals in mixtures, both within and among populations (contrast three vs. six individuals: mixed model, $F_{1,34} = 0.49$, $P = 0.490$). The composition of litter individuals had, however, no effect on decomposition rate constants (Table 2, Fig. 3a). Although litter from Kiel decomposed 10 ± 0.001 % (estimated mean ± standard error) faster overall, the diversity effect remained the same across litter from both common gardens since the common garden x diversity interaction was not significant (Table 2). Contrary to hypothesis 1, none of the litter quality variables were significantly related to decomposition rate constants on the level of single individuals and mixtures (Appendix 1 for results from simple and multiple regressions).

Synergistic responses in litter mixtures were further supported by positive values of the proportional deviation indices (observed in relation to expected decomposition rate constants) greater than zero (overall mean: 30.94 ± 7.11 %, mean ± 95 % confidence intervals). Average proportional deviation indices were always significantly greater than zero in mixtures of individuals of the same population, but only in three-individual mixtures if individuals derived from different populations (Fig. 3b). However, across all litter mixtures neither intraspecific diversity, composition nor common garden had an overall effect on proportional deviations of observed from expected decomposition (Table 2, Fig. 3b).

Discussion

Intraspecific variation in litter quality and litter decomposition

Our results showed that individuals within local beech populations vary greatly in litter quality and decomposition. This phenotypic variation among individuals is composed of genetic and environmental components (e.g. Falconer and MacKay 1996, Klaper and Hunter 1998).

Without knowing the kinship among individuals, it is not possible to quantify the contribution of genetic factors relative to the environmental component of the variation that may be caused by, e.g., small-scale environmental heterogeneity within a particular garden. By contrast, any differences among populations are likely to be genetically based, because replicate offspring from each population were randomly arranged across the same set of environmental variation. However, we found only weak differences among populations in litter quality variables, and no differences in decomposition rate. This pattern of among population variation was maintained across gardens, indicating a lack of genotype x environment interaction at the population level. The low differentiation among populations in litter quality, despite that populations were sampled over a large geographic gradient across Europe, suggests however that selection pressures on leaf traits are either very similar across populations or that litter quality is selectively neutral. High variation among individuals within populations might be maintained by balancing selection caused by spatial and temporal variation in selection pressures (Hedrick 2007). For example, genetic variation is often observed for defence traits related to herbivore pressure (Van der Meijden 1996, McIntyre and Whitham 2003), and this may potentially affect the decomposer community (but see Crutsinger et al. 2008). In this way, selection could cause greater variation within than among populations. In addition, the effect of site conditions specific to the common gardens on SLA and the C/N-ratio suggests a plastic response to environmental heterogeneity, but this was again consistent across populations, as indicated by the lack of a significant common garden x population interaction. The absence of variation in plasticity is remarkable, given that the two common gardens differ markedly in climatic conditions, with Vienna having a more continental climate compared with Kiel.

Most interestingly, the pattern of variation in phenotypic traits we observed is similar to patterns at neutral genetic markers in beech populations, where most variation is partitioned within rather than among populations (e.g. Demesure et al. 1996, Comps et al. 2001, Magri et al. 2006). Low differentiation among beech populations and high variability within them can be explained by high outcrossing rates and pronounced gene flow among populations through wind-transported

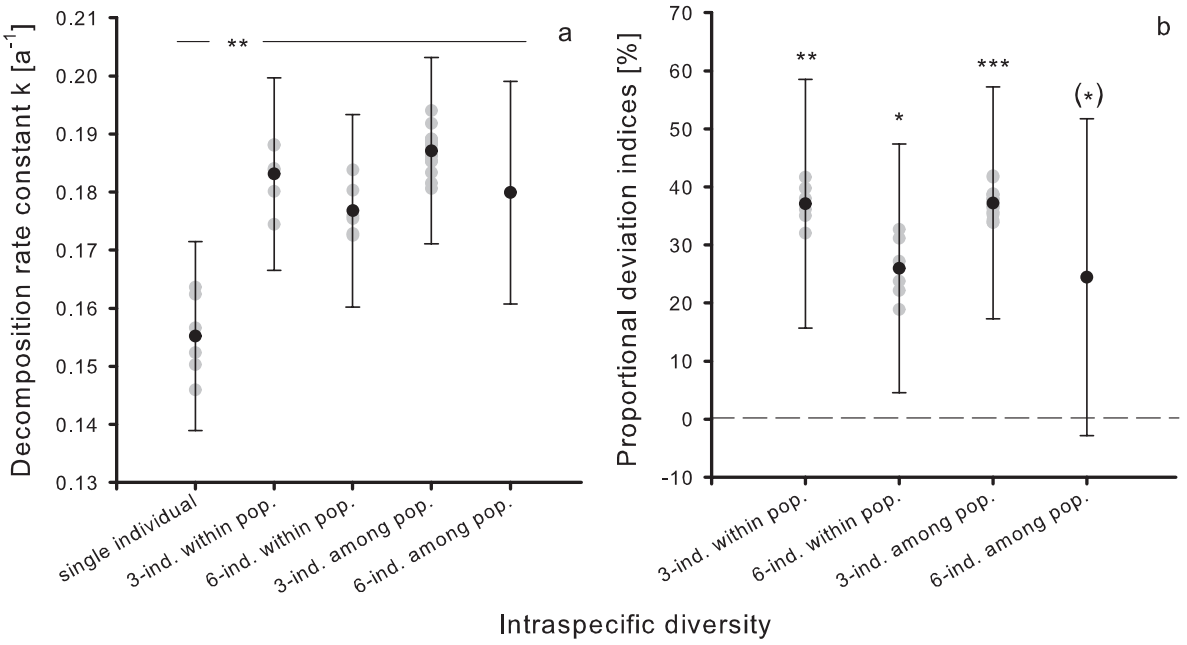

Fig. 3. Effects of intraspecific diversity on (a) litter decomposition rate constants (k) and (b) proportional deviation indices (observed in relation to expected k, with expected values calculated based on component litter individuals). Black points are (a) estimated mean k ± standard error and (b) estimated mean deviations ± 95 % confidence intervals of different individuals and mixtures (light grey points). Asterisks indicate (a) significant contrast single vs. mix and (b) significant deviation from zero (no overlap with 95 % confidence intervals). For statistical analyses see Table 2. $^{(*)}$ $P < 0.1$, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

pollen (Demesure et al. 1996) and animal-dispersed seeds (e.g. by the European jay as the main long-distance seed disperser; Nilsson 1985). The pattern of variation at neutral markers is not necessarily representative of the distribution of variation in quantitative traits (Hamrick 2004). Nevertheless, high gene flow should be a major factor considered for sustainable forest management in terms of genetic resources, since it affects the adaptive properties of both cultivated and surrounding tree populations (Lefevre 2004).

Although the genetic basis of the phenotypic variation in litter quality and decomposition among individuals within populations remains unknown, it is particularly interesting, because this may lead to potential differences in nutrient dynamics at local scales (e.g. Madritch and Hunter 2002, 2005, Schweitzer et al. 2005). Since leaf litter provides about half of the organic carbon

and nitrogen inputs to deciduous forest floors (Coleman and Crossley 1996), patches with high intraspecific diversity of beech may have higher nutrient turnover and consequently tree growth than patches of low diversity. This then could create a positive feed-back on stand productivity via enhanced decomposition.

Effects of intraspecific diversity on litter decomposition

Litter decomposition was faster at higher intraspecific diversity, as indicated by the acceleration of decomposition rate constants by 17 % in all mixtures. Whereas it would take 19 years to achieve 95 % decomposition of litter from a single individual, litter turnover time would be 16.5 years in litter mixtures (calculated as 3/k, see Didham 1998). Furthermore, positive effects of intraspecific diversity on decomposition are supported by synergistic responses observed as greater decomposition rates in litter mixtures relative to expected values based on the decomposition rates of component individuals. These synergistic responses were of a magnitude similar to those previously observed at the species level (see Gartner and Cardon 2004 for an overview). Among the non-additive effects of interspecific litter mixtures, synergistic outcomes are the most frequently reported, with mixtures exceeding expected decomposition by around 20 % or less in the majority of cases (Gartner and Cardon 2004). Here we found observed decomposition in relation to expected values to be increased by ~37 % and ~25 % in litter mixtures (three and six individuals, respectively). Non-additive effects of a similar magnitude are reported from experimental manipulation of genetic diversity within *Populus* (Schweitzer et al. 2005), while others found no or only weak effects of within-species diversity on decomposition rate (Madritch and Hunter 2005, Madritch et al. 2006). Although not further investigated, potential mechanisms may be similar to those hypothesized for processes at the species level, namely (1) homogenization of litter quality by leaching of nutrients or secondary compounds among litter individuals or (2) higher decomposer diversity and activity through increased niche space in litter mixtures (see reviews by Hättenschwiler et al. 2005, Hughes et al. 2008).

The lack of an additional effect on litter decomposition of mixing different populations compared with within populations mixtures, as well as the lack of a significant composition-effect, can be explained by the low variation among populations (i.e. because the majority of phenotypic variation resides among individuals within a population). The persistence of the intraspecific diversity effect across litter from both common gardens, however, emphasizes its relevance to ecosystem processes such as decomposition, irrespective of environmental conditions. However, our results need to be evaluated in natural beech stands over a longer period in order to assess the effects of nutrient release from the litter on forest nutrient cycling, as well as potential feedback mechanisms associated with tree performance and associated communities above- and belowground.

Effects of litter quality on decomposition

Litter quality variables were unexpectedly poor predictors of litter decomposition in our study. This was true both at the population level as well as for single individual litters and litter individual mixtures. Our results therefore contradict predictions that decomposition is faster in high nutrient content litter with low concentration of refractory organic compounds, such as phenolics (e.g. Melillo et al. 1982, Aber et al. 1990, Heal et al. 1997, Hättenschwiler and Vitousek 2000). Recently it has been shown that variation in litter quality within a single species also affects decomposition (e.g. Madritch et al. 2006, Lecerf and Chauvet 2008). Our results suggest that secondary compounds or traits other than those measured are most relevant for decomposition in European beech. Our measurements were limited to the broad chemical group of phenolics, thus ignoring chemical variation and diversity at a finer scale that may be important to litter decomposition (Harborne 1997).

Implications for ecosystem processes

Our study shows that intraspecific variation and diversity can directly influence processes at the level of communities and ecosystems. Therefore, diversity within a single species may be as important as interspecific diversity for the maintenance of ecosystem functioning, particularly in species-poor systems (McGraw 1995) such as European beech stands which often are quasi monospecific (Leuschner et al. 2009). On the other hand, intraspecific variation may be sufficiently large to override interspecific differences among co-occurring tree species. Therefore, incorporating this component in mixed litter species studies may help to clarify the idiosyncratic results observed so far (e.g. Wardle and Nicholson 1996, Wardle et al. 1997, Hector et al. 2000, King et al. 2002). Evaluating the significance of intraspecific variation and diversity in multi-species assemblages will be important for determining the functional role of biodiversity on ecosystem functioning.

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Appendix 1. Result of simple (r^2 = squared correlation coefficient) and multiple regressions (F values) on the effects of litter quality on decomposition rate constants (k [a^{-1}]), calculated on the basis of single litter individuals and mixtures ($k_{ind.\ \&\ mix.}$) and the population level (k_{pop}). D.f. = degrees of freedom, SS = sum of squares, C/N = C/N-ratio, SLA = specific leaf area [$cm^2\ g^{-1}$], phenolics = total phenolic content [$mg\ g^{-1}$]. $P > 0.1$ for all.

	$\mathbf{k}_{ind.\ \&\ mix.}$				$\mathbf{k}_{pop}$			
Source of variation	r^2	d.f.	SS	F	r^2	d.f.	SS	F
SLA	0.005	1	0.014	2.58	0.004	1	0.0001	0.09
C/N	0.002	1	0.002	0.42	0.003	1	0.0011	0.97
Phenolics	0.001	1	0.004	0.64	0.286	1	0.0014	1.22
SLA x C/N		1	0.002	0.38				
SLA x Phenolics		1	0.001	0.11				
C/N x Phenolics		1	0.001	0.13				
SLA x C/N x Phenolics		1	<0.001	0.01				
Residual		466	2.534			2	0.0023	

General Discussion

To date most studies have investigated the effects of plant diversity on primary productivity and have been performed in grasslands (Naeem et al. 1994, Tilman et al. 1996, Hector et al. 1999, Roscher et al. 2004), whereas the importance of biodiversity for ecosystem processes and functioning in forest communities remains poorly understood. This thesis was therefore motivated by a need to assess the effects of tree diversity on above- and belowground productivity and decomposition along an experimentally manipulated diversity gradient in a temperate forest system using different approaches including field and pot experiments.

In summary, I showed that total productivity was increased in mixed compared with monospecific stands and that positive effects of tree diversity were related to complementarity rather than selection (chapter 1). Tree diversity effects on productivity were density-dependent, being more pronounced at low planting density, and occurred below rather than above ground (chapter 1). Belowground competition in tree pairs was also shown to result in increased root production and allocation, although this effect did not depend on the identity of the competitor (chapter 2). Furthermore, I found that species composition of leaf litter – interactively with soil fauna – rather than litter diversity *per se* affected litter decomposition (chapter 3). Interestingly, decomposition in mixtures resulted in synergistic effects only in the absence of soil fauna, suggesting that small litter diversity effects can be masked by soil fauna activity (chapter 3). Finally, I showed that intraspecific variation and diversity have considerable effects on litter decomposition in *Fagus sylvatica* L. (chapter 4). In the following I return to the questions posed in the General Introduction in an endeavour to link and generalise the findings of this thesis and to outline areas for future research.

Does tree diversity positively affect ecosystem processes?

Overall these experiments showed that tree diversity does have positive effects on the ecosystem processes of productivity and decomposition. However, these effects were weak and generally most pronounced when comparing monocultures with mixtures. Furthermore, diversity effects of living trees on ecosystem processes were stronger compared with effects of leaf litter diversity (chapter 1 and 3).

In contrast to grasslands, studying tree diversity effects on productivity is a long-term and practically challenging task. Although within the time-frame of this thesis I was only able to consider a relatively short period limited to an early stage of tree growth, diversity effects and other factors acting upon community level processes are already of relevance in the early establishment phase. However, this phase is usually not considered in grasslands due to its shortness (Scherer-Lorenzen et al. 2007b). Furthermore, focusing on this phase has additional advantages, such enabling us to quantify the effects of tree diversity and underlying mechanisms below ground (chapter 1). This is the first time diversity effects below ground have been demonstrated for trees, and so despite the caveats of our experiment (i.e. use of pots and restriction to early stages of tree growth) provides a strong foundation for future research.

Positive effects of mixing different tree species on forest productivity have been suggested to be caused by complementarity (e.g. Cannell et al. 1992, Kelty et al. 1992, Pretzsch 2005) although our study provides the first statistical evidence that this seems indeed to be the case (chapter 1). Presently we are not able to elucidate the precise mechanisms of complementarity or the traits involved. However, we have begun to investigate potential mechanisms in cooperation with the group of Dr. Schulz from the Department of Soil Ecology at the UFZ. We tested for partitioning in nitrogen use between trees in mixture using ^{15}N labelling in liquid tracers ($^{15}NH_4$ and $^{15}NO_3$ in the tracer NH_4NO_3 provided) in the experiment described in chapter 1. Although these data

are not yet available, we hope to be able to clarify whether trees in mixture differ in their N uptake from different N sources (i.e. different chemical forms) from what would be expected from monocultures and to understand the functional diversity of N-uptake and N-utilisation in these tree communities.

Tree diversity only significantly affected total productivity via increases in below- rather than aboveground productivity (chapter 1). Furthermore the expression of the effects of diversity on productivity was dependent on confounding variables such as planting density, with diversity effects being more pronounced at low density. The latter in particular highlights the importance of competitive interactions in determining ecosystem processes, and for trees this appears to be more intense below ground. In chapter 2 we could also demonstrate an increase in root production in response to belowground competition, which might be driven by the opportunity to pre-empt the resource acquisition of neighbours. In the early stages we investigated there was no effect of root overproduction and intensified root allocation on aboveground biomass. However although our data emphasise the importance of belowground processes early in tree growth, this is not to say that aboveground processes are not important. For example, changes in branching architecture as a response to the competitive environment above ground may also be of interest (see chapter 1), particularly in later stages of tree growth. Overall, changes in allocation as a result of competitive strategies are highly significant in woody perennials, given that the large investment of their biomass in woody tissue is not reversible (Scherer-Lorenzen et al. 2005). Grasses and herbs by contrast largely renew their biomass each year and therefore allocation strategies arising from competitive interactions might not have such long-term consequences.

Overall, diversity effects were of a smaller magnitude to those usually observed in grasslands (Hector et al. 1999, Roscher et al. 2005, Spehn et al. 2005). Compared to grassland species, trees may be more plastic in their ability to use resources depending on their local environment or their niches largely overlap in terms of resource requirements, particularly in these early stages

(e.g. chapter 2). Another major difference to grassland systems is that the most competitive species potentially coming to dominate the community are not the most productive but rather are characterised by a relatively low productivity (DeClerck et al. 2005, Körner 2005 in, Szwagrzyk and Gazda 2007). Although this may become more evident over a longer time scale, our data indicate that intensified competition results in negative selection effects thus favouring species with lower-than-average monoculture yields (chapter 1). However, across all studies species composition had a stronger effect than the number of species *per s*e on ecosystem processes (chapter 1-3), thus highlighting the importance of specific species traits, which would merit further investigations, for example to determine which traits are particularly relevant.

Are diversity effects consistent across different ecosystem processes?

Although tree diversity had a positive effect on productivity, it was less important for decomposition. Therefore the effects of tree diversity are process-specific and apparently of minor importance for belowground processes such as decomposition. Weak synergistic effects of litter mixing were only found when excluding soil fauna (chapter 3). Soil fauna activity may have masked diversity effects on decomposition by selective feeding preferences being largely determined by litter quality (chapter 3). However, using litter bags in order to study the contribution of soil fauna to litter decomposition may be problematic due to confounding effects of mesh size on decomposition rates and improved methodological approaches are needed in order to solve this problem (Kampichler and Bruckner 2009).

Although it has been suggested that litter diversity indirectly influences decomposition via the decomposer community that feeds on it, the emerging pattern seems to be that plant species identity, and hence species composition, is an important driver of decomposer diversity and composition, whereas litter diversity effects are only of minor importance (e.g. Wardle et al. 1997, 2005, 2006, Bardgett and Shine 1999). It has been suggested that most soil fauna groups are rather generalist in terms of feeding and habitat preferences, hence relatively unresponsive

to subtle effects in the nature of resources created through mixing litter (Wardle et al. 2006). Furthermore, litter species diversity may not necessarily enhance resource heterogeneity, because some individual litter types might support an equally wide range of substrates and microhabitats as mixtures of many species (Hooper et al. 2000). However, additional data we collected on the diversity, composition and abundance of the decomposer fauna and microbial community in litter species monocultures and mixtures, as well as data on changes in litter chemistry during decomposition, will help to shed some light on the mechanisms underlying effects of litter diversity on decomposition. Furthermore, we tested whether there is a "home field advantage" to litter decomposition, i.e. whether specific litter types decompose faster at their site of origin. This may help to further test for the indirect effects through which tree species influence litter decomposition, e.g. by creating a unique environment in terms of chemical and physical properties thereby influencing the soil community.

The significant effect of litter species composition for decomposition found in our study indicates the importance of species specific traits and their combination for determining the rate of decomposition in mixtures (chapter 3). Mixing litter of different species may have synergistic effects on decomposition of some species mixtures but not others, and this variability potentially masks overall diversity effects. Furthermore, although overall litter diversity may not affect decomposition of the whole litter mixture, it may affect species-specific decomposition rates in mixtures (e.g. Hättenschwiler and Gasser 2005, Scherer-Lorenzen et al. 2007a). Depending on their size and variation, and although not detectable at the level of the whole litter mixture, such species specific responses might be crucial for temporal nutrient dynamics (e.g. Hättenschwiler et al. 2005). However, experimental evidence for the importance of these processes is limited, and with data collected at the species level in mixtures we hope to be able to clarify and contribute to these ideas.

Beyond stand level investigations, the next important step is to investigate performance at the individual level in terms of decomposition dynamics in mixtures as well as growth and

productivity. This is certainly possible when working with trees and will help to improve our understanding of processes operating at multiple scales. Studies by, e.g., Potvin and Gotelli (2008) and Potvin and Dutilleul (2009) have elegantly demonstrated the importance of single species performance and the local neighbourhood in determining productivity in tropical tree plantations differing in diversity. An individual centred perspective such as this will furthermore provide the possibility to consider intraspecific variability which is an important component of tree diversity as shown in chapter 4 for decomposition.

Are tree diversity effects also important at the intraspecific level?

In contrast to diversity at the species level, intraspecific diversity strongly affected leaf litter decomposition (chapter 4). Perhaps intraspecific variation was sufficiently large to override interspecific differences among litters from different species (chapter 3, 4). Furthermore, litter decomposition and quality greatly varied among individuals of a single species (chapter 4). These results contribute to the growing awareness that within-species variation and diversity can directly influence processes at the level of communities and ecosystems. Nevertheless, it is often ignored when considering ecosystem level effects of species composition (Madritch et al. 2006) and some authors even warn of being unnecessarily "fine-scaled" (Chase and Knight 2003). However, our results indicate that there is a need to evaluate the wider significance of intraspecific variation and diversity in multi-species assemblages. Spatial variation in within-species litter quality, decomposition rate and linked nutrient fluxes from decomposing litter, can furthermore be either advantageous or disadvantageous for conspecifics or other species, depending on how well the release of nutrients from the litter matches the plant's nutrient demand (Silfver et al. 2007). This in turn is likely to influence community composition (e.g. Madritch et al. 2006)(2009). Overall, intraspecific variability needs to be considered in the concept of biodiversity and ecosystem functioning and for modelling approaches, or at least caution must be exercised in interpretation of results with averaged species values (Wright et

al. 2004, Crutsinger et al. 2006). Furthermore, incorporating this component in mixed species studies may help to clarify the idiosyncratic results observed so far (e.g. Wardle and Nicholson 1996, Wardle et al. 1997, Hector et al. 2000, King et al. 2002).

The need for an integrative approach

Biodiversity can simultaneously enhance multiple ecosystem processes (Hector and Bagchi 2007). This thesis shows idiosyncratic effects of diversity depending on the process being studied, and the importance of other factors such as planting density or decomposer fauna on the expression of these effects. This emphasises the need to integrate across the multitude of processes which are influenced by diversity in order to fully understand the relationship between biodiversity and ecosystem functioning in forest ecosystems. There is not only a great need to investigate mechanisms occurring below ground more thoroughly, but also to incorporate biotic interactions above and below ground, both of a mutualistic or antagonistic nature, as well as the effects of higher trophic levels (e.g. Raffaelli et al. 2002, Duffy et al. 2007). Furthermore, an intensified consideration of the linkages and feedback mechanisms between above- and belowground processes and the interactions occurring within and among herbivore-focused and detritus-based food webs is necessary to fully understand the interaction of factors determining and driving the relationship between biodiversity and ecosystem functioning (e.g. Wardle 2002).

The challenge now is to evaluate our findings under natural conditions in more mature tree communities and over larger temporal and spatial scales. Multi-experimental and site comparisons will help to improve our understanding of the factors influencing the biodiversity ecosystem functioning relationship in forest ecosystems and to elucidate general patterns and underlying mechanisms. So far we are just beginning to assess the interacting components determining ecosystem functioning in temperate forests. However, synthesising this knowledge

and integrating it with management practices and policy will help to develop wise strategies for re-establishing biodiversity in long-term managed monoculture plantations. This will also contribute to maintaining and preserving biodiversity in the very few last stands of natural temperate forest in Europe and elsewhere, while meeting the economic aspects of forestry and insuring sustainable ecosystem functioning.

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Summary

Global changes and declines in biodiversity at all taxonomic levels have intensified the scientific effort to understand the functional role of biodiversity as a regulator of ecosystem processes. Although evidence for a positive relationship between biodiversity and ecosystem functioning is accumulating from studies mainly performed in grasslands, little is known about the importance of this relationship in forest ecosystems, despite their huge ecological and socioeconomic importance. In this thesis I therefore assessed the effects of tree diversity on above- and belowground productivity and on litter decomposition along an experimentally manipulated diversity gradient in a temperate forest system, using different approaches including field and pot experiments.

In chapter 1, I quantified the relative contributions of complementarity and selection to net effects of tree diversity on above- and belowground productivity, and assessed whether this relationship is influenced by planting density. I found that total productivity was increased in mixed compared with monospecific stands and that tree diversity effects on productivity occurred below rather than above ground and were density-dependent. Positive effects of tree diversity were related to complementarity rather than selection and were more pronounced at low planting density. This study demonstrates the potential role of niche separation in driving the biodiversity ecosystem functioning relationship in trees, and highlights the significance of belowground processes for driving this pattern.

Chapter 2 looks deeper into the role of belowground competition in affecting root allocation of saplings. I tested whether trees increase root allocation in response to the presence of neighbours, and whether this response is more pronounced in the presence of con- compared with heterospecific competitors. Although belowground competition in tree pairs led to increased root production and root allocation, this effect was independent of the identity of the competitor, perhaps because neighbour recognition mechanisms are absent in trees. Increased

root production more generally may have implications for carbon storage and nutrient retention within forest systems.

In chapter 3, I examined the functional importance of "after-life" effects of tree species diversity and its interaction with soil fauna on a crucial ecosystem process, leaf litter decomposition. In particular I investigated the relative importance of different direct and indirect pathways through which litter species diversity can influence decomposition. Different litter species compositions varied greatly in decomposition rates, which interactively with soil fauna was more important than litter diversity per se for litter decomposition. However, decomposition in mixtures resulted in synergistic effects only in the absence of soil fauna, suggesting that small litter diversity effects may be masked by soil fauna activity.

In chapter 4, I quantified intraspecific variation in litter quality and decomposition and the ecological consequences of intraspecific diversity on decomposition rates. Using European beech as a model species, I showed that there was considerable intraspecific variation in litter decomposition rates, although this was not related to litter quality. However, I also found synergistic effects on decomposition of mixing litter from different individuals, demonstrating the significance of intraspecific variation on this ecosystem process.

Overall this study demonstrates the importance of biodiversity both among and within species for ecosystem functioning. However, diversity effects were relatively weak, and species composition was a consistently better predictor of variation in productivity and decomposition. This underscores the importance of specific species traits in driving ecosystem processes in tree communities.

Zusammenfassung

Globale Umweltveränderungen und der Verlust der biologischen Vielfalt auf allen taxonomischen Ebenen haben zu einer verstärkten Anstrengung geführt, die funktionelle Rolle der Biodiversität für die Regulierung von Ökosystemprozessen zu verstehen. Während mehr und mehr Ergebnisse aus Grünland-Studien auf eine positive Beziehung zwischen Biodiversität und Ökosystemfunktion hinweisen, ist bis jetzt wenig über diesen Zusammenhang in Waldökosystemen bekannt, und das obwohl diesen Systemen beträchtliche ökologische und sozioökonomische Bedeutung zukommt. In der vorliegenden Arbeit beschäftigte ich mich deshalb mit der Wirkung von Baumdiversität auf oberirdische und unterirdische Produktivität und auf Streuzersetzung entlang eines experimentellen Diversitätsgradienten in einem gemässigten Waldökosystem und verwendete dabei verschiedene Methoden, wie zum Beispiel Feld- und Topfexperimente.

In Kapitel 1 wurden die relativen Anteile von Komplementaritäts- und Selektions-Effekten am Netto-Effekt der Baumdiversität auf die oberirdische und unterirdische Produktivität gemessen, und es wurde getestet, ob dieser Zusammenhang abhängig von der Pflanzdichte ist. Es zeigte sich, dass die Gesamtproduktivität in gemischten verglichen mit monospezifischen Beständen erhöht war, dass Diversitätseffekte eher unterirdisch als oberirdisch vorkamen und dass diese dichte-abhängig waren. Positive Diversitätseffekte waren eher auf Komplementarität als auf Selektion zurückzuführen und waren in geringer Pflanzdichte stärker ausgeprägt. Diese Untersuchung verdeutlicht die potentielle Rolle, die der Nischentrennung in der Biodiversitäts-Ökosystemfunktions-Beziehung bei Bäumen zukommt und unterstreicht in diesem Zusammenhang die Bedeutung von unterirdischen Prozessen.

Kapitel 2 betrachtet die Rolle der unterirdischen Konkurrenz für die Wurzelallokation bei Jungbäumen genauer. Es wurde getestet, ob Bäume die Wurzelallokation als Reaktion auf die Anwesenheit von Nachbarn erhöhen und ob diese Reaktion stärker ist bei con- verglichen mit

heterospezifischen Konkurrenten. Obwohl unterirdische Konkurrenz in Baumpaaren zu erhöhter Wurzelproduktion und –allokation führte, war dieser Effekt unabhängig von der Identität des Konkurrenten, möglicherweise weil Bäumen die Mechanismen zur Erkennung von Nachbarn fehlen. Erhöhte Wurzelproduktion im Allgemeinen kann Folgen für die Kohlenstoffspeicherung und das Nährstoffrückhaltevermögen in Waldökosystemen haben.

In Kapitel 3 wurde untersucht, ob die Baumdiversität auch eine Rolle spielt wenn es sich um totes Material (Streu) handelt. Hierbei wurde ausserdem getestet ob die Interaktion mit Bodenlebewesen eine entscheidende Ökosystemfunktion, nämlich die Streu-Zersetzung, beeinflusst. Im Besonderen wurde die relative Bedeutung verschiedener direkter und indirekter Wirkungspfade ermittelt, durch welche die Streudiversität die Zersetzung beeinflussen kann. Verschiedene Streuzusammensetzungen unterschieden sich stark in ihren Zersetzungsraten, was, in Wechselwirkung mit der Bodenfauna, wichtiger für die Streuzersetzung war als die Streudiversität an sich. Allerdings ergaben sich synergistische Effekte aus der Zersetzung in Mischungen nur dann, wenn die Bodenfauna ausgeschlossen wurde. Dies deutet darauf hin, dass der kleine Einfluss, den die Streudiversität hat, durch die Aktivität von Bodelebewesen überdeckt werden kann.

In Kapitel 4 wurde einerseits die innerartliche Variation der Streuqualität und Zersetzungsrate gemessen und andererseits wurden die ökologischen Konsequenzen der intraspezifischen Diversität für Streuzersetzung ermittelt. Mit der Rot-Buche als Modell-Art konnte gezeigt werden, dass es beträchtliche innerartliche Schwankungen in Streuzersetzungsraten gibt, obwohl diese nicht mit der Streuqualität zusammenhingen. Allerdings wurden auch synergistische Effekte gefunden, die durch das Mischen von Streu von verschiedenen Individuen zustande kamen, was die Bedeutung von innerartlicher Diversität für diesen Ökosystemprozess verdeutlicht.

Insgesamt verdeutlicht diese Arbeit, wie wichtig die biologische Vielfalt zwischen und innerhalb von Arten für das Funktionieren von Ökosystemen ist. Allerdings waren die gefundenen

Diversitätseffekte relativ schwach und die Artenzusammensetzung war durchgehend besser geeignet, die Unterschiede in der Produktivität und in der Streuzersetzung zu erklären. Dieses Ergebnis unterstreicht die Bedeutung von artspezifischen Merkmalen für Ökosystemprozesse in Baumgemeinschaften.

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Peer-reviewed publications

Haase J, Brandl R, Scheu S, Schädler M (2008) Above- and belowground interactions are mediated by nutrient availability. *Ecology* 89: 3072-3081.

Schädler M, Brandl R, **Haase J** (2007) Antagonistic interactions between plant competition and insect herbivory. *Ecology* 88: 1490-1498.